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Cranial Anatomy of *Hybodus basanus* Egerton from the Lower Cretaceous of England

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ABSTRACT

A detailed revision of the cranial anatomy of *Hybodus basanus* is presented. Features of the cranial and visceral endoskeleton and associated dermal elements are described. The neurocranium differs from that of modern and other fossil sharks, notably in the ethmoid and otico-occipital regions. The ethmoid regions of *Hybodus* and *Xenacanthus* are shown to be similar in some respects. The otico-occipital regions of *Hybodus* and *Xenacanthus* differ profoundly in the topographical arrangement of the otic capsule, postorbital process, and lateral otic process. Topologically, the arrangement in *Hybodus* could be obtained by telescoping the otic capsules, lateral otic processes, and occiput of a *Xenacanthus* braincase between its postorbital processes. This imagined telescoping produces a "short" otic region in *Hybodus,* but the arrangement differs from that found in modern sharks. The jaws of *Hybodus basanus* have a strong ethmoidal articulation but lack a postorbital one; limited protraction of the jaws seems to have been possible. There are five large labial cartilages in each cheek. In some respects these labial cartilages resemble those of chimaeras, and various theories of homology between shark and chimaeroid labial cartilages are reviewed. The hyoid arch is peculiar in that the hyomandibula passes dorsal to the otic ramus of the palatoquadrate. Five branchial arches are present, but only their epi- and ceratobranchials are described. A complete dentition is described and variation between the teeth is discussed; variation seems sufficient to include *H. ensis* and *H. parvidens* as synonyms of *H. basanus.* Dermal scales from various parts of the head and mouth are also described. Although the absence of critical data for most fossil sharks makes it difficult to establish a testable hypothesis of relationship, an attempt is made to compare *H. basanus* with other sharks. *Hybodus basanus* is the only Mesozoic shark in which the cranial anatomy has been studied, and the author cautions other systematists against attaching too much weight to the notion that *Hybodus* is closely related to modern sharks.

INTRODUCTION

Excellent cranial material of *Hybodus basanus* has been known for many years, being described first by Egerton (1845). Yet it was more than 70 years before Woodward (1916) published an account of its cranial morphology. Since that time, no attempt has been made to obtain further data from this material, despite its excellent state of preservation, although it has been referred to from time to time (e.g., Smith, 1942; Patterson, 1966). The purpose of the present paper is to provide new data on the cranial anatomy of *Hybodus basanus,* and to compare this form with a range of other modern and fossil sharks.

Chondrichthyan fishes have the poorest fossil record of any major vertebrate group. Throughout their geological history, chondrichthyans usually are represented only by micromeric dermal scales, isolated teeth, and spines. With few exceptions (such as in menaspoids and some myriacanthoids), well-developed macromeric dermal armor has not been a chondrichthyan hallmark. Additionally, the characteristic prismatically calcified perichondral layer of the chondrichthyan endoskeleton is extremely fragile in comparison with the bony endoskeleton of many other gnathostomes. Consequently, endoskeletal remains of fossil chondrichthyans are uncommon and are usually disarticulated and fragmentary. As if this were not bad enough, however, there is ample evidence that on past occasions paleontologists have failed to recognize prismatically calcified skeletal remains for what they are, even where these are well preserved (Maisey, in preparation). For many years, the only detailed studies of Paleozoic shark neurocrania were those of Gross (1937), Stensiö (1937), and Romer (1964), and the only account of Mesozoic *Hybodus* cranial anatomy was that of Woodward (1916, 1919).

Renewed interest in the comparative anatomy and systematics of Recent elasmobranchs (e.g., Compagno, 1973, 1977; Nakaya, 1975; Springer, 1979; Maisey, 1980) has fortuitously coincided with a period of great discovery regarding fossil chondrichthyans (e.g., Zangerl, 1969, 1979; Zangerl and Case, 1973, 1976; Lund and Zangerl, 1974; Lund, 1974; Schaumberg, 1977; Baird, 1978; Dick, 1978; Dick and Maisey, 1980). Many of the taxa described in these works are new to science, and their interrelationships will undoubtedly be the subject of lively debate for years to come. Little substantial progress is likely, however, until the systematics and

interrelationships of Recent sharks, rays, and chimaeras are refined, and until detailed comparative studies of the more complete fossil chondrichthyans are made (e.g., Schaeffer, 1981). Already it is evident that there is as much diversity in the cranial anatomy of Paleozoic sharks as there is among modern ones.

Hybodus customarily occupies an important position in systematic studies of sharks. It is a common Mesozoic genus and is known from numerous unusually well-preserved specimens of Jurassic and Cretaceous age. *Hybodus* is similar to other Mesozoic genera, such as *Acrodus, Asteracanthus, Lissodus,* and *Palaeobates,* and it is generally agreed that all these forms are closely related (e.g., Day, 1864; Woodward, 1889a; Brown, 1900; Koken, 1907; Zittel, 1911; Stromer, 1927; Brough, 1935; Peyer, 1946; Patterson, 1967; Rieppel, 1981; Maisey, 1982). These sharks (loosely termed "hybodonts") have on occasions been considered the ancestors of some or all modern sharks (see below). In comparison with most fossil sharks, *Hybodus* and its allies are fairly well known (e.g., Brown, 1900; Koken, 1907; Woodward, 1916; Rieppel, 1981). By contrast with anatomical studies of modern sharks, however, those dealing with *Hybodus* are superficial and frequently misleading. Inevitably, fossil taxa will be known in less detail than extant ones, yet as knowledge of modern sharks increases it is possible to obtain more comparative morphological data from the fossils.

Acknowledgments

Many people have directly or indirectly helped bring this project to fruition. I am indebted to Dr. Colin Patterson, British Museum (Natural History) for permitting me to work on the specimens of *Hybodus basanus* and for much advice and discussion. Initial preparation of specimens took place at St. Albans' College, England, and I thank my colleagues there for their helpful assistance. Subsequently the specimens were worked on in the American Museum of Natural History by Mr. Walter Sorensen and Ms. Lorraine Meeker (who also drafted the illustrations), and photographs were taken by Mr. Chester Tarka. Dr. Bobb Schaeffer has been an oracle of wisdom, and I am extremely grateful for his continued encouragement.

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Abbreviations

INSTITUTIONAL:

AMNH, American Museum of Natural History
BM(NH), British Museum (Natural History)
CMNH, Cleveland Museum of Natural History
GSM, Geological Survey and Museum (United Kingdom)
PU, Princeton University
UM, University of Michigan
UNMNH, University of Nebraska, Natural History Museum
USNM, National Museum of Natural History, Smithsonian Institution

ANATOMICAL:

acv, anterior cerebral vein
add f, adductor fossa
art cot, articular cotylus
art k, articular knob
art lab, articular labial
art pr, articular process
asc, anterior semicircular canal
au lab, anterior upper labial
bh, basihyal
buc VII, buccal ramus of facial nerve
cbr, ceratobranchial
ch, ceratohyal
cik, caudal internasal keel
da, dorsal aorta
den gr, dental groove
dr pr, dorsal rostral process
ebr, epibranchial
ect pr, ectethmoid process
eha, efferent hyoidean artery
end f, endolymphatic (parietal) fossa
epsa, efferent pseudobranchial artery
ethp pr, ethmopalatine process
facv, foramen for anterior cerebral vein

fa v, facial vein
feha, foramen for efferent hyoidean artery
fep, epiphyseal foramen
fepsa, foramen for efferent pseudobranchial artery
fhyp, hypophyseal foramen
fica, foramen for internal carotid artery
flda, foramen for lateral dorsal aorta
fm, foramen magnum
fonv, foramen for orbitonasal vein
fora, foramen for orbital artery
fpal VII, foramen for palatine ramus of facial nerve
fson, foramina for spino-occipital nerves
fsoph V, foramina for superficial ophthalmic ramus of trigeminal nerve
gica, groove for internal carotid artery
glda, groove for lateral dorsal aorta
gora, groove for orbital artery
hotl, hypotic lamina
hsc, horizontal semicircular canal
hym, hyomandibula
hym art, hyomandibular articulation (braincase)
hym VII, hyomandibular branch of facial nerve
ica, internal carotid artery
im con, internal mandibular concavity
imr, internal mandibular ridge
int s, internasal septum
ioc, infraorbital canal
jc, jugular canal
lab, labial cartilage(s)
l com, lateral commissure
lda, lateral dorsal aorta
loph VII, lateral ophthalmic ramus of facial nerve
lot pr, lateral otic process
lw lab, lower labial
Mc, Meckel's cartilage
mxa, maxillary artery
mx V, maxillary ramus of trigeminal nerve
nas cap, nasal capsule
nas font, nasal fontanelle
oc cot, occipital cotylus
olf c, olfactory canal
onv, orbitonasal vein
opa, optic artery
opha, ophthalmic artery
ophv, ophthalmic vein
or, orbit
ora, orbital artery
orv, orbital vein
ot cap, otic capsule
pal pr, palatine process (palatoquadrate)
pnw, postnasal wall
po pr, postorbital process
pq, palatoquadrate
prcf, precerebral fontanelle
prcf', precerebral fossa (*Xenacanthus*)
prf com, prefacial commissure
prof V, profundus branch of trigeminal nerve
psc, posterior semicircular canal
pu lab, posterior upper labial
q con, quadrate concavity
q fl, quadrate flange
rb, rostral bar
sub s, suborbital shelf
sup c, supraorbital (laterosensory) canal
sup cr, supraorbital crest
tfr, trigemino-facialis recess
II, optic nerve
III, oculomotor nerve
IV, trochlear nerve
V, trigeminal nerve
VI, abducens nerve
XII, facial nerve
IX, glossopharyngeal nerve
X, vagus nerve

Materials and Methods

Hybodus basanus was first discovered in the Atherfield Clay (lower Cretaceous) of the Isle of Wight, in southern England (Egerton, 1845), but many subsequent discoveries were made elsewhere (fig. 1), notably near Bexhill on the Sussex coast (Woodward, 1889a). These remains include many uncrushed heads and some postcranial fragments, first described by Woodward (1916, 1919). Although the general collecting locality is known, the precise horizon is open to doubt. In a letter to Woodward dated May 26, 1915, Charles Dawson wrote: "If I remember rightly Beckles got his *Hybodus* from Cooden about two miles west of Bexhill, in Pevensey Bay but six or seven miles from Pevensey. Being a long-shore specimen it is of course difficult to fix the horizon. . . . It is by no means certain that Beckles' specimen came from the upper Wealden but it is quite 25 years since I saw this specimen. It is quite likely to be Ash(down) Sand."

Woodward (1916, p. 10) ignored Dawson's information, however, and some lower Wealden teeth and spines resembling those of *H. basanus* were not referred to that species, which Woodward thought was restricted to the "Weald Clay" (which at that time included the Atherfield Clay). Patterson (1966, p. 292) also restricted *H. basanus* to the Weald Clay (Barremian) and Atherfield Clay (lower Aptian).

The discovery of ostracods (fig. 26), identified as *Cypridea wicheri torosa* Anderson, in the matrix of a Bexhill *H. basanus* head,

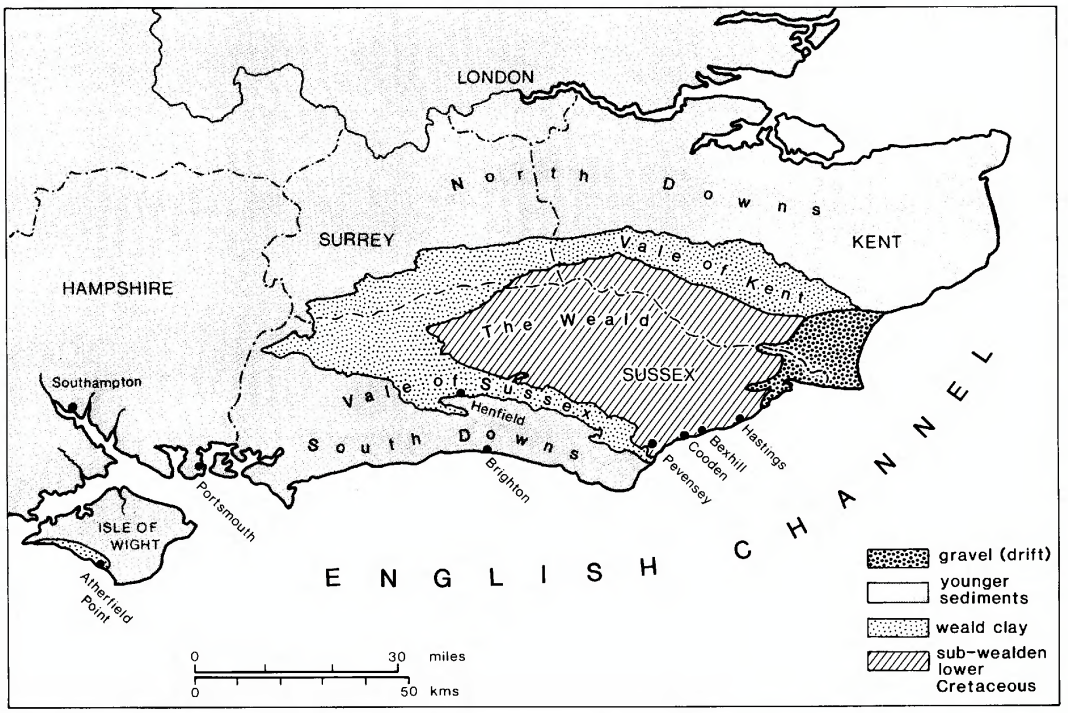


FIG. 1. Simplified geological map of south-eastern England showing *Hybodus basanus* localities mentioned in text.

suggests that Dawson correctly surmised the stratigraphic level from which this material came. This ostracod ranges throughout the upper Purbeck series and is prolific (up to 14% of the ostracod population) in the Bexhill ostracod cycle of the lower Wealden (Valanginian), including the Ashdown Sand, but it is not recorded at higher stratigraphic levels (Anderson, 1971). The demonstrated range of *H. basanus* (Valanginian to lower Aptian) is therefore much greater than Woodward (1916) and Patterson (1966) supposed. This discovery is significant for two reasons. Firstly, some Wealden species of *Hybodus* based on isolated teeth were originally distinguished from *H. basanus* largely on stratigraphic grounds that are now untenable (see section below on teeth). Secondly, *Cypridea* is typically a brackish to fresh water ostracod (Anderson, 1971), and *H. basanus* may therefore have been able to tolerate a wide range of salinity, from fully marine (Atherfield Clay) to virtually fresh water (Ashdown Sand).

Improved preparation techniques provide an opportunity to reexamine *H. basanus* specimens previously considered physically intractable because they are embedded in a partially silicified ironstone matrix. They are preserved in three dimensions, often with minimal distortion. Even previously "useless" specimens have taken on new significance now they have been prepared, although only unsilicified matrix has yielded to thioglycollic (mercaptoacetic) acid treatment (for techniques see Howie, 1974).

In order to revise the cranial anatomy of *H. basanus,* I have examined all the specimens in the British Museum (Nat. Hist.) collections. These were also available to Woodward, no new specimens having been acquired in the intervening years. Most of this material is listed by Woodward (1889a) and is not therefore itemized again here. However, certain specimens require further mention.

The holotype of *H. basanus* is not in the British Museum but is a Geological Survey specimen, GSM 27973. One of Beckles's

specimens was exchanged by the British Museum and sent to the American Museum in 1967 [formerly one of a series catalogued as BM(NH) P6356, is now AMNH 4692]. The only specimen now designated P6356 is shown in figures 6, 7, 21, and 22. Two of the better specimens available to Woodward are BM(NH) P11870 and P13094, and his (1916) restoration is largely based on these.

Much additional information has now been obtained from BM(NH) 40718 and P60110, both of which are now extensively prepared. BM(NH) 40718 has been dismantled so that its neurocranium can be examined. Although its dorsal surface (fig. 2A) is badly weathered, other regions are well preserved. The main importance of this specimen is the information it yields regarding the orbits, ethmoid region, and basicranium (figs. 2, 3, 10). The occiput is damaged, however, and P60110 was prepared in order to discover more about that region. This specimen exceeded all expectations, since not only is the occiput well preserved (fig. 5), but the dorsal part of the braincase also reveals many interesting features, and the jaws and hyomandibula of the left side appear to be properly articulated. The right visceral elements are crushed over to the left and are damaged. Also, despite a generally good state of preservation, the orbital walls of P60110 are damaged. Therefore, P40718 remains the only reliable source of information concerning the orbit, and is so far the only specimen which clearly shows the inner surface of the palatoquadrates.

The neurocranium of AMNH 4692 is badly damaged and provides little information, but preparation of its jaws revealed a complete dentition (fig. 7), which provided a basis for the restoration shown in figure 18. The entire roof of the buccal cavity is covered in scales, and removal of the basihyal revealed the scales covering the "tongue." We have therefore gained some information about the distribution and variation of oropharyngeal scales in *H. basanus.*

In addition to the specimens of *H. basanus,* I have been able to examine a semi-articulated Liasic hybodontid [BM(NH) P50869] which has been acid prepared to display its otico-occipital region and jaw suspensorium. I have also examined casts or peels of Brown's (1900) *H. fraasi,* Koken's (1907) *H. hauffianus,* Teixeira's (1956) *H. cassangensis,* K. S. Thomson's (unpublished) Madagascan hybodont, specimens of *Lissodus africanus,* and specimens of an undescribed late Carboniferous hybodont from Kansas.

HISTORY OF HYBODONT SYSTEMATICS

The type species of *Hybodus, H. reticulatus,* is based on teeth (Agassiz, 1837), but another species, *H. incurvus* (based on a finspine), was thought to be synonymous. Subsequently, more complete remains of other species were described, e.g., the crushed neurocranium and jaws of *H. delabechei* (Woodward, 1889b), complete and partial skeletons of *H. hauffianus* (Fraas, 1889, 1896; Koken, 1907), *H. fraasi* (Brown, 1900), and heads of *H. basanus* (Egerton, 1845; Woodward, 1916, 1919). Although Agassiz placed *Hybodus* and *Acrodus* in separate families, he was no doubt aware of Owen's histological studies (published in 1840) showing that both genera have osteodont teeth. Day (1864) showed that *Acrodus anningiae* had finspines like those attributed to *Hybodus.* Subsequently, many authors have placed these genera close to *Heterodontus* ("*Cestracion*"), because of similarities in the teeth of *Acrodus* and *Heterodontus.* For example, Woodward (1889a) placed *Heterodontus, Hybodus, Acrodus,* and various other Mesozoic and Paleozoic genera into a family Cestraciontidae, which was united with all living "asterospondylous" sharks, but was separate from remaining "cyclospondylous" forms (squaloids, *Squatina,* and batoids). Elsewhere, Woodward (1886b) suggested that hexanchoids and *Chlamydoselachus* were derived from *Hybodus.* This concept is almost as recurrent in the literature as the hypothesis of a relationship with *Heterodontus,* and is based on supposed similarities between the jaws of hexanchoids, *Synechodus,* and *Hybodus* (e.g., Woodward, 1886a, 1898; Brown, 1900; Goodrich, 1909; Smith, 1942). These hypotheses went a long way in establishing the long-held view that *Heterodontus, Chlamydoselachus,* and hexanchoids are very primitive modern sharks.

Zittel (1911) first separated *Hybodus* and its allies from modern elasmobranchs, although he maintained that *Hybodus*

belonged to the group which gave rise to modern forms. Brough (1935) took this view further, and attempted to show that hybodonts and modern sharks were only distantly related. Moy-Thomas (1939a, 1939b) also retained hybodonts as a separate group. Curiously, in later years *Heterodontus* has crept back into the taxon containing *Hybodus* (e.g., Berg, 1955; Young, 1962; Patterson, 1967; Blot, 1969), although in only one of these classifications (Blot, 1969) have the hexanchoids and *Chlamydoselachus* also been included with *Hybodus*. Up to the present time, therefore, there is no agreement as to whether hybodonts form a monophyletic group if modern sharks are excluded. Taking earlier hypotheses of relationship, and couching them in cladistic terms we find that Woodward (1889a) considered squaloids, *Squatina,* and batoids to be the sister group of *Hybodus* and remaining modern elasmobranchs. Furthermore, he made hexanchoids the sister group of *Hybodus, Heterodontus,* and galeomorphs (*sensu* Compagno, 1973). Glikman (1964) regarded *Hybodus* and lamnoids as a sister group of other modern elasmobranchs. Brown (1900) and Goodrich (1909) made hexanchoids the sister groups of *Hybodus* and remaining living elasmobranchs. Whereas Brown (1900) separated *Hybodus* from non-hexanchoid modern forms, however, Goodrich (1909) united *Hybodus* and *Heterodontus*. According to Brough (1935) and Moy-Thomas (1939a, 1939b), *Hybodus* is the sister group of all modern elasmobranchs (neoselachians of Compagno, 1977). Another popular view is that batoids are the sister group of *Hybodus* and modern sharks (e.g., Regan, 1906; White, 1937; Romer, 1945; Berg, 1955; Patterson, 1967).

Since *Hybodus* is founded on isolated teeth (Agassiz, 1837), there is always some possibility that the form studied here is not closely allied to the type species. Elsewhere (Maisey, 1982), I have shown that earlier confusion of the fossil selachian *Synechodus* with *Hybodus* created a major obstacle in trying to elucidate the relationships of *Hybodus* and modern elasmobranchs (see Smith, 1942). How "typical" of Mesozoic hybodonts is *H. basanus*? Its tooth morphology is consistent with that of Jurassic hybodonts, including *H. reticulatus* (the type species), and in many other respects its dermal scales, cephalic spines, and finspines are like those of Jurassic forms. Moreover one specimen of *H. reticulatus,* BM(NH) P2203d, consists of teeth associated with an occipital region which, as far as can be determined, closely resembles that of *H. basanus*. Therefore it is not unreasonable to suppose that *H. basanus* resembles many other Mesozoic hybodonts in its cranial anatomy; a preliminary comparison with *H. hauffianus, H. fraasi,* and *H. delabechei* corroborates this view (Maisey, 1982), which can be tested as further remains are discovered.

THE NEUROCRANIUM

General Features

In profile, the neurocranium is weakly wedge-shaped (figs. 2–5, 8, 9). The orbitotemporal region inclines steeply down toward the nose, but the basicranium slopes forward only slightly. From the front, the head has an almost mammalian expression, produced by the large, downturned postorbital processes which superficially resemble an incomplete zygomatic arch (po pr, figs. 3D, 6B, 8D, 9D). The maximum width of the neurocranium (between the postorbital processes) is only slightly less than its length. This is not apparent in many specimens, however, as the postorbital region often was damaged by erosion and therefore seems narrower. The orbits are ovoid and the supraorbital shelf is well developed. Woodward's (1916) restoration does not show the postnasal wall correctly, or the slight forward inclination of the distal part of the postorbital process. These features give the orbit an oval rather than semicircular shape. The precerebral fontanelle is rounded and the olfactory capsules were placed a moderate distance apart.

The cranial morphology of modern elasmobranchs is somewhat variable (Garman, 1913; White, 1937; Holmgren, 1941; Compagno, 1973, 1977). Forms such as *Notorhynchus, Chlamydoselachus, Squatina, Scyliorhinus,* and *Odontaspis* have broad, squat braincases, in which the orbit takes up a third or more of the total length, and which are generally broadest at the level of the postorbital processes. In many of these forms

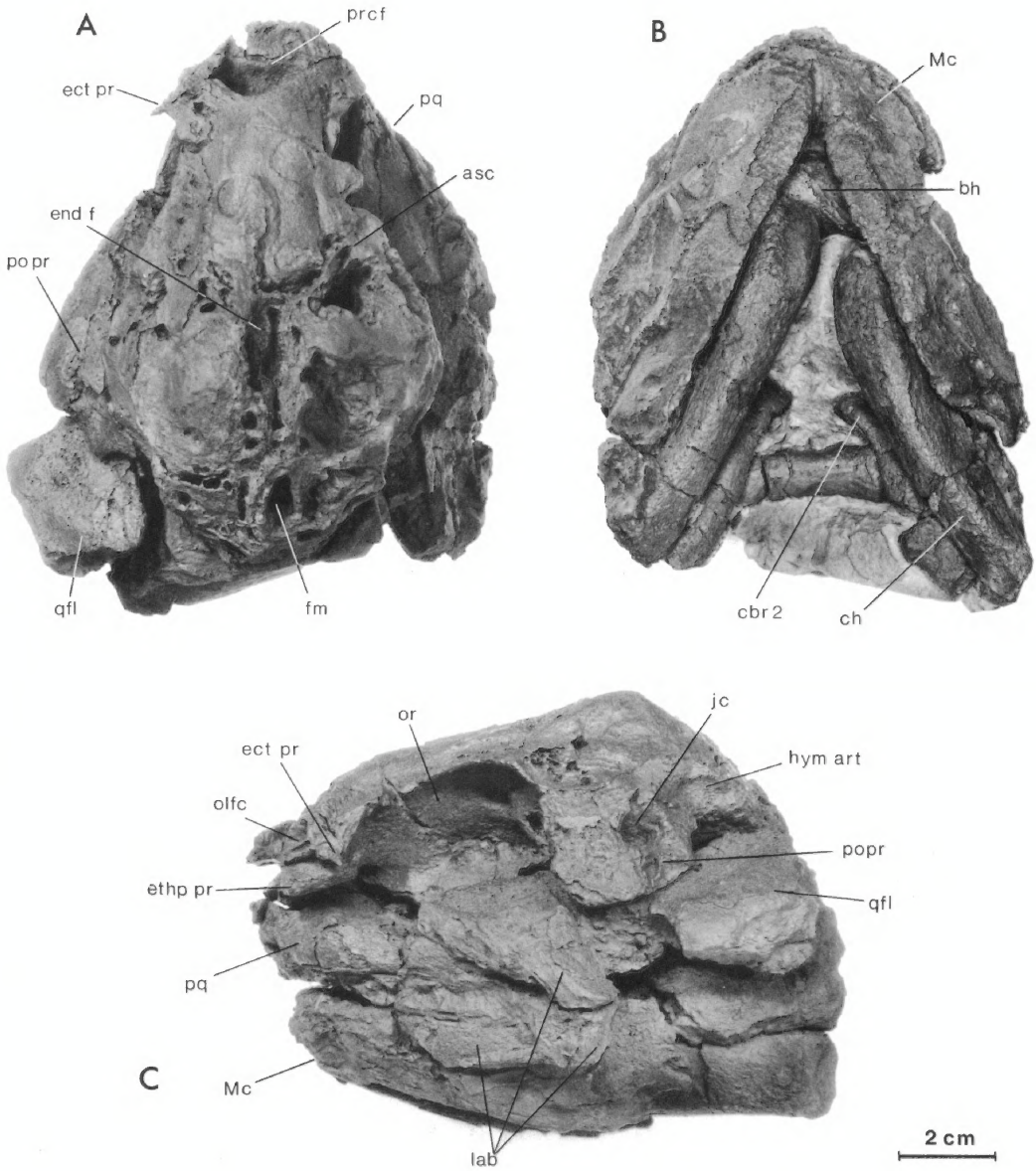


FIG. 2. *Hybodus basanus,* BM(NH) 40718; cranium and jaws in (a) dorsal; (b) ventral; and (c) left lateral views.

(*Odontaspis* excepted), a rostrum is weakly developed. In all these forms, the precerebral fontanelle is fairly broad, and the olfactory capsules are well separated from each other, especially in *Squatina* (Iselstoger, 1937). In many other modern elasmobranchs, the precerebral fontanelle is relatively narrow, and the mesial walls of the olfactory capsules more nearly approach the midline, e.g., *Scymnorhinus, Oxynotus, Etmopterus, Somniosus, Heptanchus, Mustelus, Chiloscyllium, Heterodontus, Isurus,* and *Urolophus.* In *Heter-*

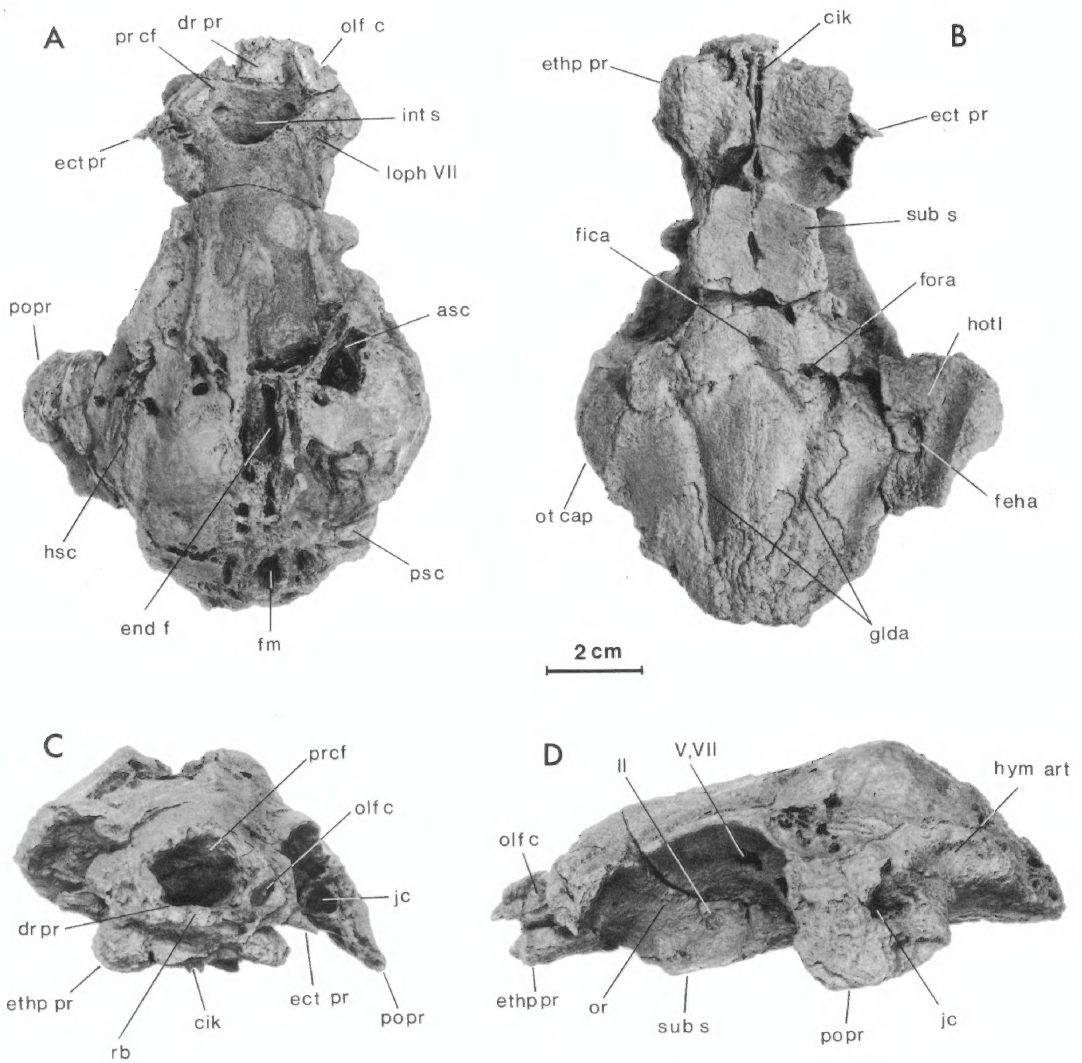


FIG. 3. *Hybodus basanus,* BM(NH) 40718; braincase only, in (a) dorsal; (b) ventral; (c) anterior; and (d) left lateral views.

odontus, Orectolobus, and *Rhiniodon* the neurocranium has a somewhat rectangular outline in dorsal view, because the width across the postorbital processes is virtually equaled by the width across the olfactory capsules. To some extent this is also true in *Squatina,* and in *Pristiophorus* and batoids the postorbital processes are reduced, so that the broadest part of the neurocranium is across the olfactory capsules. In lamnoids, the postorbital process generally forms the broadest part of the neurocranium (e.g., *Cetorhinus, Lamna, Isurus, Carcharodon*), although in *Odontaspis, Alopias,* and *Mitsukurina* the postnasal wall may be almost as broad as the postorbital region. In carcharhinids, the postorbital process is small; in specialized forms, such as *Sphyrna,* the postnasal wall is greatly expanded laterally, contributing to the characteristic hammer-shaped head.

Among fossil sharks, there is also consid-

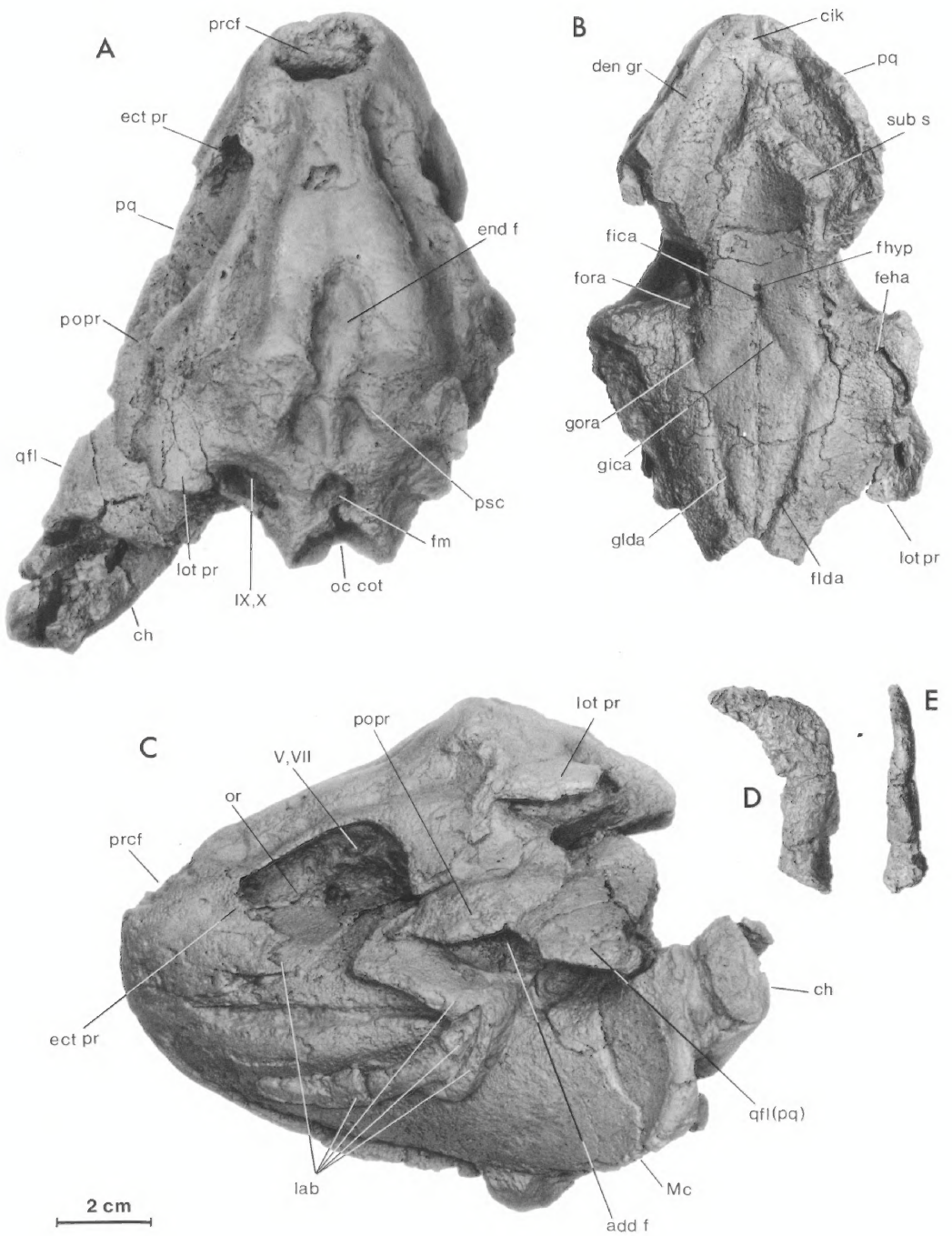


FIG. 4. *Hybodus basanus,* BM(NH) P60110; cranium and jaws in (a) dorsal; (b) ventral; and (c) left lateral views. Note that the anterior portions of the palatoquadrate remain *in situ* in (b), but the remainder of the jaws have been removed. Hyomandibula of this specimen is shown separately in (d) left lateral and (e) posterior views.

erable variation in the overall form of the braincase (fig. 15). In *Xenacanthus* and *Tamiobatis,* the postorbital process forms the broadest region, although Schaeffer (1981, figs. 5, 6) restores *Xenacanthus* with slightly broader lateral otic processes; the difference is not great, however. "*Cladodus*" *wildungensis* has been restored similarly (Schaeffer, 1981, figs. 12, 25), although the size of the lateral otic processes is unknown. In *Cobelodus,* the postorbital processes form delicate arcades only slightly broader than the postnasal wall (Zangerl and Case, 1976). The postorbital processes of *Tristychius* also form a delicate arcade, but this is reinforced ventrally by broad suborbital shelves (Dick, 1978, fig. 9). In most of these fossil sharks, the precerebral fontanelle is relatively as wide as in *Hybodus,* and the olfactory capsules are correspondingly far apart. In *Cobelodus,* however, and to some extent in *Tristychius,* the precerebral fontanelle is narrow in relation to its length, and the olfactory capsules seem to have been closer together than in *Hybodus basanus, Xenacanthus,* and *Tamiobatis.*

Comparing the braincase of *H. basanus* with those of other fossil and Recent sharks, most agreement in general morphology is found with *Xenacanthus* and *Tamiobatis,* apart from certain peculiarities of *Hybodus* (particularly in the ethmoid and otico-occipital regions, discussed later). There are important differences in the relative lengths of these braincases, and in the relative positions of the otic capsules, postorbital processes, and lateral otic processes. Nevertheless, if a braincase like that of *Tamiobatis* is imagined to undergo a topological modification by shunting the entire otico-occipital region forward between the postorbital processes (so that the otic capsules lie between the postorbital processes), the end product would be very much like the braincase of *H. basanus.* The orbitotemporal and ethmoid regions of *H. basanus* closely resemble those of *Xenacanthus* and *Tamiobatis,* apart from bulbous ethmopalatine processes (see below), which have developed on either side of the internasal plate in *H. basanus.*

Ethmoid Region

In both specimens of *H. basanus* where the ethmoid region (including olfactory canals

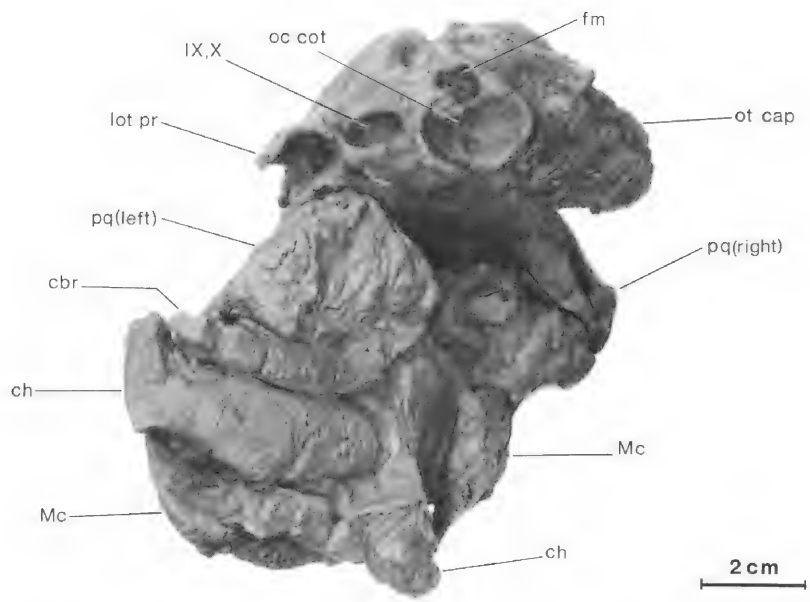


Fig. 5. *Hybodus basanus,* BM(NH) P60110, in posterior view.

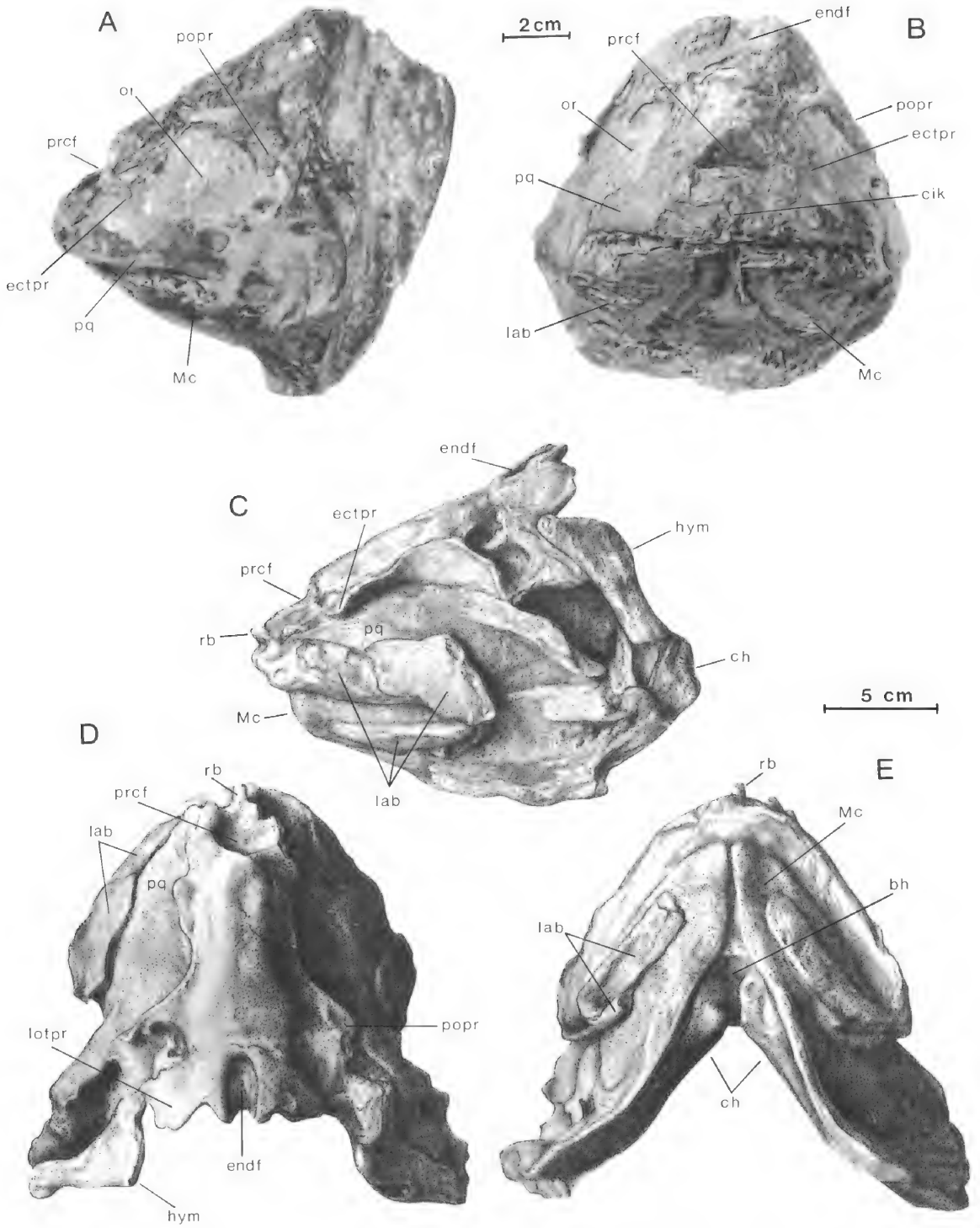


FIG. 6. *Hybodus basanus* specimens; (a, b) BM(NH) 6356 in left lateral and anterior views; (c, d, e) BM(NH) P11870 (after Woodward, 1916).

and rostrum) has been prepared [BM(NH) 40718 and P60110], the neurocranium is well calcified (figs. 2C, 3, 4A, C, 10, 13, 14). These specimens are considerably smaller than the largest [BM(NH) P31726], which suggests that the ethmoid region became calcified relatively early in development. It is not possible to establish whether this region was among the last to calcify, as it is in *Squalus* (Benzer, 1944). Smaller specimens of *Xenacanthus* also have well calcified ethmoidal regions (Schaeffer, 1981).

The ethmoid region of *H. basanus* contributes to only about one-quarter of the whole length of the braincase (figs. 8, 9), and is therefore comparatively shorter than in most living sharks. In *Tristychius,* however, the ethmoid region also constitutes only a quarter of the braincase length (Dick, 1978), and in *Cobelodus* (Zangerl and Case, 1976), *Tamiobatis* (Romer, 1964), and *Xenacanthus* (Schaeffer, 1981) the proportion is even lower (fig. 15).

Nasal capsules are not well preserved, and consequently their former extent in *H. basanus* can only be guessed at. The olfactory canals are quite short, but are wide, suggesting that nasal capsules were well developed, and that the olfactory sense was fairly acute (olf c, figs. 3, 9, 10). The nasal capsules would have been spaced widely apart (fig. 12d) and separated by a broad internasal lamina (Jarvik, 1942), which forms the floor (=*solum cavi praecerebralis* of Allis, 1913) of the precerebral fontanelle (*cavum praecerebrale*). The ventral portions of the olfactory canals are visible in BM(NH) 40718 as anterolaterally directed depressions on each side of the internasal plate (fig. 10C). There does not seem to have been a calcified mesial wall to these canals, so that they now appear to be continuous with the precerebral fontanelle. The broken margin of a cartilaginous roof over the nasal capsule is visible on the right side of BM(NH) 40718. In this area there is also evidence for the floor of a canal, probably for an anteromedially directed branch of the lateral ophthalmic nerve, which was presumably enclosed by cartilage for more of its length than in modern elasmobranchs. Immediately behind the vicinity of the olfactory canal are other foramina defining the position of a more lateral branch of the same nerve. In most of the specimens of *Xenacanthus* studied by Schaeffer (1981), postmortem damage has obliterated traces of the precerebral fossa opening into the cranial cavity. In UM 16194 and PU 22391B, however, calcified cartilage extends ventrally from the rim of the precerebral fontanelle (prcf) defining a smaller precerebral fossa (prcf', figs. 11, 14). *Xenacanthus* is unusual in having this part of the cranial roof folded inward. In some lamnoids the precerebral fossa is almost completely closed by cartilage, however, leaving only an opening for the pineal organ, e.g., *Cetorhinus.*

In the rim of the precerebral fontanelle of *Xenacanthus* is a pair of foramina. One of these has been traced back to the canal for the lateral ophthalmic nerve in UM 16194 (loph VII, fig. 11). A comparable branch of this nerve has not been reported in modern elasmobranchs but may have been present in *Hybodus* (above). There is little hope of recognizing it in fossils where the fontanelle wall is not inflected, unless (as in *H. basanus*) a canal for the nerve is preserved.

The anterolateral margin of the internasal septum in *H. basanus* is recessed at the external opening of the olfactory canal into a broader cavity. This would have housed either the olfactory bulb or the entire capsule (olf c, figs. 10, 12D, E). Posterior to this recess, the internasal septum (int s, figs. 3, 9, 10) merges with a short dorsal process (dr pr, discussed at length below). The relationships of this recess to the above-mentioned structures suggest that it represents the inner margin of a nasal fontanelle, which in *Chlamydoselachus* is said by Allis (1923, p. 132) to be homologous with the *fenestra choanalis* of amphibians, despite the absence of a choanal tube (Jarvik, 1942, p. 252). There is no evidence for a cartilaginous bridge defining the lateral wall of the nasal fontanelle and separating it from the *fenestra endonaria* in *H. basanus*; if present, it was probably too delicate to preserve. Remains of the olfactory capsule itself, or of an *ala nasalis,* have not been found.

The anterior part of the internasal septum is exposed beneath the precerebral fontanelle in BM(NH) 40718, but its anterior extremity is incomplete. Anteriorly, the dorsal surface

of the internasal septum (the dorsal rostral process, dr pr, fig. 3) is produced into a short rostral bar (rb, figs. 3C, 10C, 12D, E), an essentially separate feature from the caudal keel (cik) which lies farther ventrally (see below). It is the rostral bar which is figured as a curious bump on the snout by Woodward (1916, text fig. 3; pl. II, fig. 1; see fig. 6C here). The anterior margin of the precerebral fontanelle is defined by the front of the internasal septum, as in *Chlamydoselachus,* and is upturned slightly (relative to the rest of the fontanelle floor, fig. 12A). In BM(NH) 40718, this floor is crossed by an almost straight transverse ridge, corresponding to the level at which large ethmopalatine processes (discussed below) meet the ventral surface of the internasal septum (fig. 10C). It is uncertain whether this ridge was present in life, or whether it is an artifact produced by downward distortion of the rostral process. The cartilage is broken in places along this ridge, however, suggesting that some distortion has occurred.

A few millimeters behind this transverse ridge, a pair of small foramina penetrate the floor of the fontanelle (fig. 10C, facv). These foramina are peculiar in lying so far forward in the basicranium. In specimens of *Xenacanthus* examined by Schaeffer (1981) the fontanelle floor was not well preserved, but in UM 16194 this area is intact (fig. 11), and there is evidence of anteriorly positioned foramina, as in *H. basanus.* Not enough of the fontanelle floor is preserved in *Tamiobatis* to determine whether this form was similar. The ethmoid region is also incomplete in "*Cladodus*" specimens (Stensiö, 1937; Gross, 1937). In *Tristychius,* the ethmoid region is known in some detail (Dick, 1978), but the floor of the anterior fontanelle has not been described. Zangerl and Case (1976) have described some features of the endocranial wall in *Cobelodus,* but were unable to examine the ethmoid region. The foramina in the fontanelle floor of *H. basanus* open laterally into short canals before turning posterolaterally. They also give off anteriorly directed rami which apparently end blindly, although their precise courses are difficult to follow without destroying the specimen. Further discussion of these canals and foramina is left until the ethmoid region is described more completely (see below).

In *Hybodus basanus,* the ventral surface of the internasal septum is folded into a median caudal keel (cik, figs. 3B, 4B, 8B, 9B, 10A, 12E, F, 13A). The floor of the precerebral fontanelle is not folded into this keel. Thus the dorsal surface of the internasal septum is not involved in the caudal keel, but remains relatively flat. The caudal keel of *H. basanus* closely resembles that of *Xenacanthus* and *Tamiobatis* (cf. fig. 13A, B). Schaeffer (1981) identifies this caudal keel as part of the rostrum in *Xenacanthus,* fused with the internasal septum, postnasal wall (="preorbital processes") and nasal capsules.

The ontogeny of rostral structures in modern elasmobranchs can vary considerably, but the medial parts at least seem to originate as forward outgrowths of the trabeculae (e.g., *Scyliorhinus,* De Beer, 1937, p. 52; *Squalus,* Holmgren, 1940; Jollie, 1971) although the median rostral keel thus formed often chondrifies separately from the rest of the braincase.

In *Hybodus basanus,* the median internasal keel is separated from the anterior lip of the precerebral fontanelle by an embayment in the cartilage. The keel is therefore ventral to that part of the cranium corresponding to the "rostral bar" (Jarvik, 1942) of *Chlamydoselachus,* in which a median internasal keel is absent even in the earliest embryos studied (Holmgren, 1941).

It therefore appears that the internasal keel of *H. basanus, Xenacanthus,* and *Tamiobatis* corresponds with the ventral part of the internasal septum of modern elasmobranchs. While various rostral structures are developed from the internasal septum in modern forms, however, there is no evidence that the internasal keel of *Hybodus* and *Xenacanthus* contributed to the rostrum. Instead there is evidence that the keel is actually situated farther ventrally than the rostrum of modern elasmobranchs (fig. 12B, E). The dorsal rostral process of *H. basanus* is more likely the equivalent of the median rostral element in modern elasmobranchs. The ventral keel in *H. basanus, Xenacanthus,* and *Tamiobatis* seems to represent an important structure in relation to jaw support in the ethmoid region (see below). In *Tristychius,* the ventral surface of the ethmoid region is poorly known, but has been restored completely flat, with no trace of a median keel (Dick, 1978). The pal-

atoquadrates are restored meeting at the midline beneath the rostrum, however, and there is evidence of a strong ethmoidal articulation ("orbital" process of Dick, 1978) on the palatoquadrate. How this would have articulated with a flat ethmoid region is unclear. In *Cobelodus,* the ethmoid region is very short, and appears to be located a long way ventral to the spatulate rostrum (Zangerl and Case, 1976). The internasal septum is deep, but is shorter than in *H. basanus, Xenacanthus,* and *Tamiobatis,* and a ventral keel is apparently absent.

Beneath the dorsal rostral process of *H. basanus* and arising essentially from the sides of the caudal keel are large, bulbous swellings (ethp pr, figs. 3B–D, 8B–D, 9B–D, 10, 12E, F, 13A, 14A). These are termed ethmopalatine processes, because of their position and their relationship with the palatoquadrates. The ethmopalatine processes lie ventral to the precerebral fontanelle and to the nasal capsules. At the posterior ventrolateral margin of the postnasal wall (Jarvik, 1942, = "antorbital wall" of other authors) is another, smaller dorsal ethmoidal process, which is separated from the ethmopalatine process by a deep, anteroposteriorly oriented groove. The identity of these processes is discussed further below. Posteriorly the ethmopalatine process flairs into the postnasal wall and does not contribute to the more dorsal process.

The ventral surface of the caudal keel merges with lateral palatobasal ridges, which form suborbital shelves (sub s, figs. 3, 13). The keel is separated from the ethmopalatine process on each side by a deep, rounded groove or depression (fig. 8C, D), which is occupied by the dorsal margin of the palatine ramus of the palatoquadrate (fig. 16). Considerable buttressing of the jaws against the ethmoid region is therefore evident in *H. basanus,* and Woodward's (1916) statement that the "pterygoquadrate cartilage (is) not articulated with the preorbital region of the skull" is untenable. In addition to this support given to the palatoquadrates, these elements are also buttressed against each side of the caudal keel farther anteriorly (figs. 3B, 4B, 16).

In the preceding paragraphs, the topographic relationships of the lateral processes on the ethmoidal region of *H. basanus* were discussed, but further comments on their identity are called for. We have seen that there are two prominent processes, one (the ethmopalatine process) arising laterally from the internasal wall, and a smaller one extending posterolaterally from the margin of the postnasal wall. This smaller process resembles the ectethmoid process of *Chlamydoselachus* in this respect.

The position of the orbitonasal canal is important, since DeBeer (1931) noted that cartilage lateral to it "is the *planum antorbitale,* springing from the *lamina orbitonasalis* or ethmoid process." His *lamina orbitonasalis* corresponds to the *processus antorbitalis* of Gaupp (1905) and Goodrich (1930), according to Jarvik (1942), who points out that the *lamina orbitonasalis* forms only part of the postnasal wall, and is merely an embryonic process of the trabecula.

In *Hybodus basanus* [BM(NH) 40718], there are several small foramina in the postnasal wall, and their interpretation is therefore a little ambiguous (figs. 8C, 9C, 10B, 12E, 13A). Before these foramina are discussed, some attention will be given to the innervation and vascularization of the ethmoid region in Recent elasmobranchs.

The ethmoid region of *Chlamydoselachus* has, according to Allis's (1923) and Jarvik's (1942) accounts, three principal groups of nerves and blood vessels passing through or around it (fig. 12B, E). There is a superficial group of structures, comprising the maxillary artery, facial vein, and *rami buccalis lateralis* and *maxillaris* V. These all pass lateral to the ectethmoid process, although the vein and artery send branches mesially into the nasal vacuity, via an aperture in the lateral margin of the nasal fontanelle (see Jarvik, 1942, figs. 2, 4). Within the orbit is a dorsal group of structures, including the ophthalmic artery and vein, and the *ramus ophthalmicus lateralis,* all passing through the preorbital canal. More centrally in the orbit, the postnasal wall is penetrated by the orbitonasal and anterior cerebral veins and by the profundus nerve. In *Chlamydoselachus,* the profundus nerve and anterior cerebral vein are close together, and their foramina may be confluent (Iselstoger, 1937; Holmgren, 1941). These differences may be accounted for by a slight shift in the profundus nerve relative to the blood vessels. In other Recent sharks (except *Squatina,* see below) the profundus nerve, orbito-

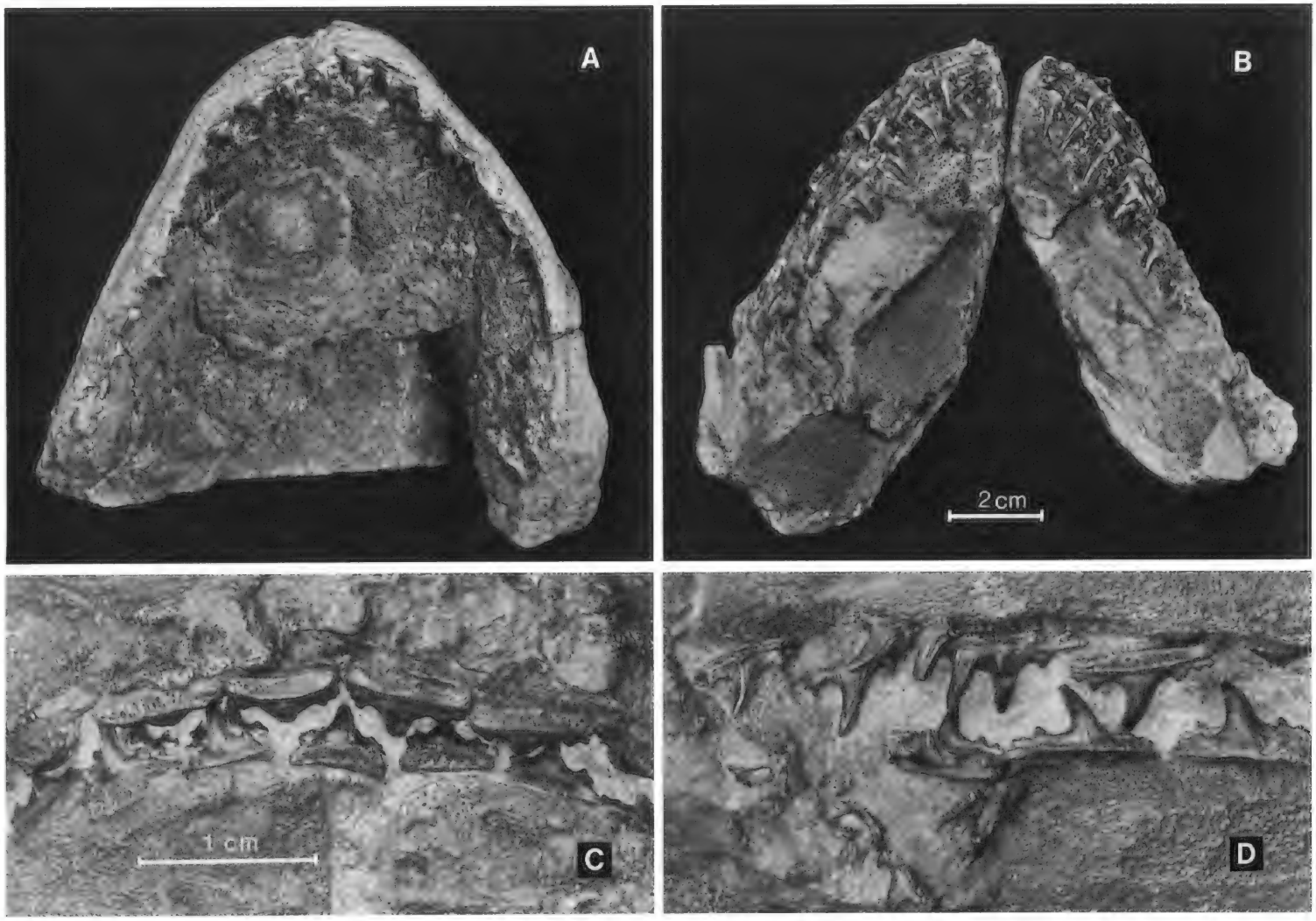


FIG. 7. *Hybodus basanus* teeth; (a, b) AMNH 4692, (a) upper dentition; (b) lower dentition, both in place on jaws. Oropharyngeal scales also visible in (a); (c, d) BM(NH) P6356, details of (c) symphyseal region and (d) left lateral teeth at corner of mouth.

nasal vein, and anterior cerebral vein enter the postnasal wall separately.

BM(NH) 40718 does not show the orbital opening of the preorbital canal at all clearly, but it is more readily discernible in BM(NH) P60110. *Hybodus basanus* therefore probably had a preorbital canal like that of modern sharks. Although we may infer that other structures, such as *buccalis lateralis* VII and *maxillaris* V, maxillary artery and facial vein also lay superficial to the chondrocranium, there is no direct evidence for these (fig. 12D–F).

Above and immediately behind each large ethmopalatine process in BM(NH) 40718, a foramen opens into a canal which passes anteriorly and then starts to swing mesially within the cartilage on each side of the postnasal wall. Without damaging the specimen irreparably, it was impossible to trace these canals for their full extent, but (as far as can be determined) they come close to meeting other posterolaterally directed canals running from the peculiar pair of foramina in the floor of the precerebral fontanelle (figs. 9, 10, facv) mentioned earlier. These foramina do not penetrate the internasal septum ventrally and cannot therefore represent small basal communicating canals. The foramina each lie in a gentle concavity leading toward the olfactory region, and are probably situated in the floor of the olfactory canal (fig. 10C). Comparison with *Chlamydoselachus* (Jarvik, 1942, fig. 3) suggests that the anterior cerebral veins passed from the olfactory canal via these foramina in the fontanelle floor (fig. 12A, D). This interpretation implies that the area referred to as the "fontanelle floor" of *H. basanus* is in part intracranial, and that the actual extracranial area was more restricted in life. Furthermore, this interpretation suggests that the foramen close to the posterior end of the ethmopalatine process contained the anterior cerebral vein. This vessel would thus have left the cranial cavity farther laterally than in any modern elasmobranch.

Other foramina in the postnasal wall are small and not well preserved in BM(NH) 40718. They are studied best under ultraviolet light. There may have been separate foramina for the orbitonasal vein and profundus nerve, although it is difficult to distinguish their foramina from small areas of broken cartilage, and only one foramen on each side is well preserved. Thus we cannot rule out the possibility that both orbitonasal vein and profundus nerve passed through a common foramen, as in *Squatina* (Iselstoger, 1937). Another possibility is that the profundus nerve entered the postnasal wall, but that the orbitonasal vein ran along the deep groove between the dorsal ectethmoid process and more ventral ethmopalatine process. I think that this is unlikely, in the light of DeBeer's (1931) comments (see above), since this would imply that there is no cartilaginous *planum antorbitale* lateral to the orbitonasal vein, and that consequently an ectethmoid process like that of Recent sharks is absent in *H. basanus*. This would leave the process I have identified as an ectethmoid without an explanation. As a further possibility, the anterior cerebral and orbitonasal veins may have combined within the postnasal wall, to share a common exit into the orbit on their way toward the orbital sinus. In support of this, the canal in the postnasal wall appears to divide, one branch turning mesially toward the foramina and canals in the floor of the precerebral fontanelle, whereas the other branch passes anteriorly toward the nasal cavity. In *Chlamydoselachus,* the orbitonasal canal penetrates the postnasal wall and its vein emerges into the nasal cavity but is separate from the anterior cerebral vein. I do not think the anterior branch of this canal in *H. basanus* contained the profundus nerve (although such a condition prevails in *Squatina*), because the canal does not emerge on the surface behind the nasal cavity, but rather seems to pass into it. In figure 12E the orbitonasal vein, anterior cerebral vein, and profundus nerve are shown with separate foramina.

As already mentioned, *H. basanus* lacks a basal communicating canal (=subnasal or rostral fenestra; Schaeffer, 1981). These openings are typical of squaloids, *Heptranchias,* and *Pristiophorus* (Holmgren, 1941) but other modern elasmobranchs lack them. Basal communicating canals are also absent in *Xenacanthus, Tamiobatis,* and "*Cladodus*" (Schaeffer, 1981). According to Dick (1978), these canals are absent in *Tristychius.* Radiographs of *Cobelodus* neurocrania enabled

Zangerl and Case (1976) to establish that its ethmoid region is short and blunt, with an opening (the precerebral fontanelle) dorsally, but without other openings. It is therefore concluded that basal communicating canals were also absent in *Cobelodus.* Available data consequently suggest that basal communicating canals are present only in certain modern sharks. It has been suggested that the presence of these openings is related to the size of the nasal capsules (Holmgren and Stensiö, 1936; Holmgren, 1941; Jarvik, 1942). It has also been proposed that the basal communicating canal is a synapomorphy of some modern sharks (Maisey, 1980).

It is possible to make detailed comparisons between the postnasal walls of *H. basanus,* BM(NH) 40718, P60110, and *Xenacanthus* sp., PU 22391B. The last specimen has only part of the postnasal wall intact (pnw, figs. 13B, 14B), but is undistorted by compaction, unlike most other *Xenacanthus* specimens. There is a large foramen for the preorbital canal, and also three smaller foramina, which seem to correspond with those for the profundus nerve, orbitonasal vein, and anterior cerebral vein in most modern elasmobranchs (*Chlamydoselachus* and *Squatina* excepted; see above). The inferred presence of a canal for the orbitonasal vein in *Xenacanthus* suggests, according to DeBeer's (1931) criteria, that an ectethmoid process was present (cf. Schaeffer, 1981). The internasal keel of *Xenacanthus* tapers rapidly forward beneath the postnasal wall, as in *H. basanus.* The keel is somewhat deeper and narrower in PU 22391B than Schaeffer's (1981, fig. 8A) restoration suggests (fig. 13B). Examination of *H. basanus,* BM(NH) 40718 and *Xenacanthus* sp., PU 22391B, in section shows how similar the depth and width of the ventral internasal keel is in these forms (fig. 13). The most significant difference between them is the presence of a broad ethmopalatine process on each side of the internasal keel in *H. basanus.* Nevertheless, in *Xenacanthus* the postnasal wall bulges laterally, above the internasal keel, before merging with the interorbital septum farther posteriorly, thus forming a deep sulcus on each side of the ethmoid region, ventral to the posterior margin of the precerebral fontanelle. This sulcus would have housed the palatine ramus of the palatoquadrate, and corresponds to the groove beneath the ethmopalatine process of *H. basanus.* The ethmoid regions of *H. basanus* and *Xenacanthus* are therefore similar, apart from the presence of the larger ethmopalatine process in *H. basanus.*

Dick (1978) interpreted a process on the postnasal wall of *Tristychius* as a "preorbital process," but did not determine the location of the orbitonasal vein. Nevertheless, from the general form and position of this process, it seems reasonable to regard it as an ectethmoid process. No comparable process has been described in *Cobelodus* or *Cladoselache,* perhaps for preservational reasons.

The epiphyseal foramen of *H. basanus* is located in the dorsal midline, just behind the precerebral fontanelle (fep, figs. 3A, 8A, 9A). A separate epiphyseal foramen also occurs in modern squaloids, hexanchoids, and scyliorhinids, but is absent in *Heterodontus,* triakids, most carcharhinids, lamnoids, and orectoloboids. It is also absent in "*Cladodus,*" *Tamiobatis,* and *Xenacanthus* (Stensiö, 1937; Gross, 1937; Romer, 1964; Schaeffer, 1981), *Tristychius* (Dick, 1978), and apparently also in *Cobelodus* (Zangerl and Case, 1976). In those forms without a separate epiphyseal foramen, the pineal organ may have lain within the posterior margin of the precerebral fontanelle, as in *Chiloscyllium* and *Orectolobus* (Holmgren, 1941, figs. 40, 42). There is some evidence for this in *Xenacanthus* (figs. 11, 14).

The structure of the ethmoid region in *Hybodus* and *Xenacanthus* suggests that Jarvik's (1942, pp. 387, 388) conclusions regarding the ethmoid region of porolepiform osteichthyans and sharks require some modification. In at least two respects, the ethmoid regions of *Hybodus* and *Xenacanthus* resemble those of porolepiforms more than that of *Chlamydoselachus*; a median caudal keel is developed in the ventral expansion of the internasal septum (fig. 9, cik), and the palatoquadrates do not meet at a strong symphysis. These similarities are interpreted here as primitive gnathostome characters, which are apomorphically lost or modified in *Chlamydoselachus* and other modern elasmobranchs. This apomorphic condition of the ethmoid region in *Chlamydoselachus* therefore exacerbates rather than emphasizes the

differences between the snout of porolepiforms and sharks, which are thus primitively more alike than Jarvik (1942) supposed. This conclusion casts doubt upon the phylogenetic significance of some of the similarities which Jarvik (1942, 1980) noted between the ethmoid region of porolepiforms and other osteichthyans, including tetrapods.

When the ethmoid regions of *Hybodus* and *Porolepis* are compared (e.g., Jarvik, 1942, fig. 37; cf. figs. 10, 12, here) some interesting similarities are noted. In *Porolepis* the ventral internasal wall is fairly narrow from side to side, and bears a median toothed parasphenoid. The ethmosphenoid which bears the parasphenoid is similar to the anterior part of the internasal keel of *Hybodus,* apart from the absence of a parasphenoid in the latter. On either side of the ethmosphenoid of *Porolepis* there is an elongate autopalatine fossa which according to Jarvik (1942, p. 361) was developed for the articulation of the anteromedial part of the palatoquadrate. A corresponding fossa in *Hybodus* also forms an articulation with the anteromedial part of the palatoquadrate. The *crista suspendens* of *Porolepis* forms the roof of the autopalatine fossa, in much the same way as the ethmopalatine process defines the dorsal limit of the corresponding fossa in *Hybodus.* In *Porolepis* the *crista suspendens* appears to be a ventrolateral extension of the olfactory ridge, within which the olfactory canal is located. The ethmopalatine process of *Hybodus* differs from the olfactory ridge of *Porolepis* in this respect, since the olfactory canal of *Hybodus* is situated farther dorsally in the internasal wall. Nevertheless, the *crista suspendens* of *Porolepis* and the ethmopalatine process of *Hybodus* are essentially similar, and may be tentatively regarded as homologous structures. Extensive development of this process in *Hybodus* is probably apomorphic, but (as fig. 13 shows), a corresponding process is present in *Xenacanthus.* Although corresponding features to those found in *Porolepis* also occur in osteolepiforms such as *Eusthenopteron* (e.g., Jarvik, 1942, figs. 47–50), the degree of similarity to sharks such as *Hybodus* and *Xenacanthus* is much less. The *crista suspendens* is narrow and fairly low in *Eusthenopteron.* It is more clearly separated from the olfactory ridge than in *Porolepis,* however, and in this respect resembles a weaker version of the ethmopalatine process of *Hybodus.*

Orbitotemporal Region

The orbitotemporal region comprises the interorbital wall, which contains the cranial cavity and the orbital roof (*tectum orbitale* of Jarvik, 1942). Much of the basicranium is included in the ventral part of the interorbital wall, and there are in *H. basanus* substantial suborbital shelves. The postorbital processes are excluded from this part of the account, since their relationship to other structures is unusual and merits separate discussion (below).

Woodward (1916) was unable to describe any features within the orbit. It is now possible to examine the excavated orbits of BM(NH) 40718 and P60110 (figs. 2C, 3D, 4C, 13A, 14A). The latter specimen has less well-preserved orbits, which have suffered from buckling and distortion, but some salient features in the better-preserved orbits of BM(NH) 40718 can be confirmed. Differences in the width of the orbital roof of various specimens of *H. basanus* (Woodward, 1919) can be discounted as being a result of imperfect preservation in the case of supposedly "narrow" examples.

There is a median temporal convexity, on either side of which is a pronounced sulcus penetrated by foramina. These supplied the supraorbital laterosensory canals with innervation from the superficial ophthalmic ramus of the facial nerve. The sensory canals would have passed from the otic region forward to the sides of the olfactory area. Their exact course is a little unclear here, but they presumably met an infraorbital canal [there is evidence of foramina supplying this canal near the anterior margin of the postorbital process in BM(NH) P60110 and 40718, and of an otic branch running toward the lateral line canal].

Most of the orbital foramina were easily located (figs. 9C, 13A, 14A) but some of the smaller ones were visible only under ultraviolet light, since the matrix within them fluoresces a pale cream or orange, in contrast with the deep purple of the cartilage. Their

FIG. 8. Restoration of *Hybodus basanus* braincase in (a) dorsal; (b) ventral; (c) left lateral; (d) anterior; and (e) posterior views. Features are identified in figure 9.

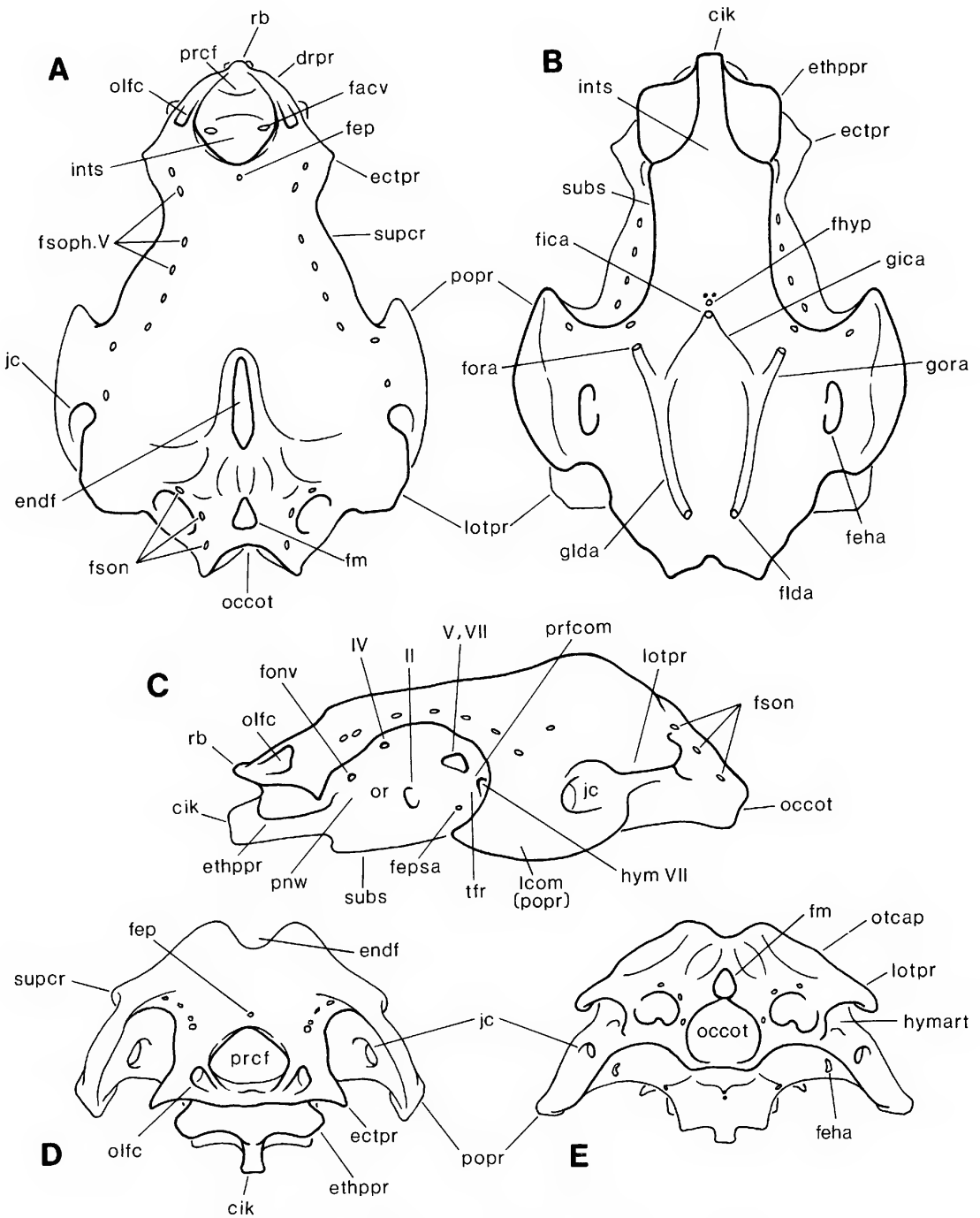


FIG. 9. Key to features on braincase shown in figure 8.

arrangements agree essentially with that of modern elasmobranchs and fossils such as *Xenacanthus* (see below), *Tamiobatis,* and "*Cladodus,*" although there are discrepancies in the interpretation of various foramina in the published accounts of the fossils (cf. Gross, 1937; Stensiö, 1937; Romer, 1964; Schaeffer, 1981).

The optic nerve and artery probably emerged together just below the center of the orbit through an oval foramen (II, figs. 3, 9, 13). Below and slightly behind this is a single foramen, which probably housed the efferent pseudobranchial artery (f epsa). There is no indication of a separate ophthalmic foramen, and the ophthalmic and efferent pseudobranchial arteries probably diverged after leaving the neurocranium, as in living sharks. Gross (1937) and Stensiö (1937) interpret "*Cladodus*" *wildungensis* as having separate foramina for these vessels. Schaeffer (1981) interprets *Xenacanthus* and Romer's (1964) *Tamiobatis* accordingly, although Romer could not locate an ophthalmic foramen. Gross (1937) found two different conditions of the ophthalmic/pseudobranchial vessels in his "*Cladodus*" specimen.

There is a deep trigemino-facialis recess (Allis, 1923) behind the optic nerve in *H. basanus* (tfr, fig. 14A). Lateral to this fossa, the orbital artery entered the orbit via a foramen in the suborbital shelf. An opening for the pituitary vein has not been located. The depth of the trigemino-facialis recess suggests that it housed the posterior rectus muscles, i.e., it probably functioned as a myodome. Schaeffer (1981) considers this the function of a similar fossa in *Xenacanthus* (fig. 14B). In *H. basanus* there is no evidence for an eye-stalk attachment.

A small foramen just below the sensory pits in the roof of the orbit of BM(NH) 40718 is probably for the trochlear nerve. Schaeffer (1981, fig. 6) placed the exit for this nerve much farther forward in *Xenacanthus,* but in PU 22391B there is evidence for a trochlear foramen close to the superficial ophthalmic foramen as in *H. basanus* and modern sharks (fig. 14). Comparison of these specimens suggests that the supposed trochlear foramen in Schaeffer's (1981) restoration of *Xenacanthus* may be for the profundus nerve. In *H. basanus* two small foramina lie close to the dorsal margin of the trigemino-facialis recess (fig. 14A). The anteriormost of these foramina (III) seems to correspond with the oculomotor foramen in *Notorhynchus* and *Chlamydoselachus.* The more posterior one is interpreted as the abducens foramen (VI), indicating the position of the *pila antotica.* In *Xenacanthus* corresponding foramina are present in PU 22391B (fig. 14B). An eye-stalk (if present) should have arisen near here, but in *H. basanus* the calcified cartilage is unbroken, which should not be expected were an eye-stalk originally present. Schaeffer (1981) found no evidence for an eye-stalk in *Xenacanthus,* although Gross (1937) interpreted the attachment area for one in "*Cladodus.*"

On leaving the braincase, the hyomandibular nerve of *H. basanus* seems to have passed abruptly backward in a groove (hym VII) before it entered the jugular canal (jc). The prefacial commissure (prf com, fig. 13) is correspondingly short. Behind the optic foramen, and above the trigemino-facialis recess is a large, anteriorly directed foramen, probably for the combined superficial and deep branches of the ophthalmic trunk. Lower down, lying dorsolateral to the trigemino-facialis recess, is a laterally directed opening which probably housed the infraorbital trunk (combined maxillary branch of the trigeminal and buccal branch of the facial nerve). Higher still in the orbit are numerous small foramina which penetrate the supraorbital ridge for the innervation of the supraorbital sensory canal from the superficial ophthalmic nerve.

Comparison with *Xenacanthus* (PU 22391B) reveals an essentially similar configuration (figs. 13, 14). The main difference between the orbits of *Xenacanthus* and *H. basanus* is that in the former the postorbital process is positioned approximately level with the trigemino-facialis recess, which is therefore obscured by the postorbital process in lateral view (fig. 13B). In *H. basanus,* the postorbital process is situated farther back, so that the trigemino-pituitary fossa is visible in lateral view (fig. 13A), giving the orbit a more elongated appearance than in *Xenacanthus* (*H. basanus* is more like "*Cladodus*" *wildungensis* in this respect). Thus in *Xenacanthus* many of the orbital foramina seem

farther back in the orbit than in *H. basanus,* but their overall positions relative to one another are comparable in both forms. The optic foramen is located toward the back of the orbit in *Xenacanthus.* There are two small foramina ventral and slightly posterior to the optic foramen. According to Schaeffer's (1981) detailed study of sectioned specimens, these foramina are for the separate ophthalmic and efferent pseudobranchial arteries. The trigemino-pituitary fossa of *Xenacanthus* is as deep as that in *H. basanus.* In *Xenacanthus* it continues posteriorly and laterally as a deep groove, into the jugular canal. In *H. basanus* a narrower groove occupies the same position in BM(NH) 40710. The function of this groove in *Xenacanthus* and *H. basanus* is uncertain, but it may have formed a path for the pituitary vein, emerging from the interorbital wall within the trigemino-facialis recess, on its way toward the lateral head vein, which it probably met within the jugular canal of the postorbital process (fig. 14). As Schaeffer (1981, p. 19) noted, a similar groove is absent in *Chlamydoselachus*; in fact, it seems to be absent in all modern sharks, including *Squatina* (the only extant elasmobranch possessing a complete jugular canal surrounded by a calcified lateral commissure; Iselstoger, 1937; Holmgren, 1941). In "*Cladodus*" *wildungensis* there is only a weak groove running from the trigemino-pituitary fossa to the jugular canal (Schaeffer, 1981, fig. 7). No such groove is known in *Tristychius* or *Cobelodus.*

The Basicranium

The anterior part of the suborbital shelf in *Xenacanthus* has a series of articular ridges, corresponding to another series on the palatoquadrate (figs. 13B, 14B). These ridges are absent in *H. basanus.* Articular ridges are known to occur in *Tamiobatis* and "*Cladodus*" (Stensiö, 1937; Gross, 1937; Romer, 1964; Schaeffer, 1981), and *Cobelodus* (Zangerl and Williams, 1975; Zangerl and Case, 1976), but are apparently absent in *Tristychius* (Dick, 1978) and were not noted by Dean (1909) or Harris (1938) in *Cladoselache.* The orbital articulation of modern squaloids, hexanchoids, pristiophoroids, *Squatina,* and *Chlamydoselachus* (orbitostylic sharks of Maisey, 1980) superficially resembles the articulation in the anterior part of the orbit of *Xenacanthus, Tamiobatis,* "*Cladodus,*" and *Cobelodus.* It is possible that these articulations are primitively homologous, in that both are forms of palatobasal articulation, but the orbital articulation of modern sharks is distinctive and consistent in its relationship to nerves and blood vessels within the orbit. This pattern is different from that seen in the fossils (Maisey, 1980). It is therefore important to distinguish the orbital articulation of modern orbitostylic sharks from other palatobasal (ethmoidal) articulations found in more primitive gnathostomes (cf. Jarvik, 1977, 1980).

The floor of the interorbital wall in *H. basanus* broadens rapidly backward from the caudal keel, with which it is confluent anteriorly (sub s, figs. 3B, 4B, 8B, 9B, 10A). According to DeBeer (1931, p. 608) in *Scyliorhinus* a separate blastemic center, close to the *lamina orbitonasalis,* becomes incorporated into the trabecular floor of the neurocranium, and is involved in the "basal" (ethmoidal) articulation with the palatoquadrates. In *H. basanus,* a corresponding center may be represented by the triangular anterior parts of the suborbital shelves. The basicranium is gently concave from side to side in this region (fig. 10B), as far back as the median internal carotid foramen. Farther posteriorly, the basicranium is faintly convex, with a trace of a median "seam" suggesting a line of fusion between parachordals (figs. 3B, 4B).

Anterior to the carotid foramen is a smaller median opening for the hypophyseal duct (f hyp), which therefore remained open in adult *H. basanus.* An open hypophyseal duct also occurs in *Xenacanthus, Tamiobatis,* "*Cladodus,*" and *Cladoselache,* but becomes closed off in adult neoselachians. The closed condition may therefore represent a neoselachian synapomorphy. The cartilage surrounding the hypophyseal foramen of *H. basanus* is ridged by faint, radiating striae which are seen best under extremely oblique lighting. Furthermore, there are two very small pits in front of the hypophyseal foramen in P60110 (figs. 4B, 9B). They seem too symmetrical to be damaged areas, but their function is unknown. The region around the hypophysis is one of the last to chondrify in developing selachian neurocrania (DeBeer, 1931), and it

is possible that this region was incompletely formed in P60110.

A pair of shallow grooves extends posterolaterally from the internal carotid foramen (fica). Each groove meets another, which extends posteriorly from a foramen located anteriorly in the floor of the suborbital shelf, just in front of the postorbital process (figs. 2B, 3B, 9B). The more mesially situated grooves presumably housed the internal carotids (gica), whereas the lateral ones housed the orbital arteries (gora). Where they merge, the single grooves would have housed lateral aortae (glda). A restoration of the basicranial circulation pattern is shown in figure 25A. The position of the efferent hyoidean arteries is somewhat speculative, but they may have passed through fenestrae in the floor of the postorbital process (see below). Aortic impressions also occur in *H. hauffianus,* but have remained unrecognized until recently (Maisey, 1982). Both Brown (1900) and Koken (1907) figured ventral views of the neurocranium, in which grooves for the lateral aortae are visible, but the neurocrania were misinterpreted as being seen in dorsal view. Aortic grooves can also be seen in a partial basicranium (*Hybodus* or *Acrodus* sp.), BM(NH) P3356, from the Lias of Yorkshire, England, in another partial head, BM(NH) P50869, from the Lias of Lyme Regis, and in an incomplete occiput of *H. reticulatus,* BM(NH) P2203d (Maisey, in preparation). In all these forms, the lateral aortae seem to have been positioned beneath the basicranium for much of their length, as in *H. basanus,* and were enclosed by short canals only adjacent to the occipital cotylus. According to Dick (1978), the lateral aortae were fully exposed beneath the basicranium of *Tristychius,* as in modern sharks. In other fossil sharks, including *Xenacanthus, Tamiobatis,* and "*Cladodus,*" the lateral aortae are enclosed by canals in the basicranium for a considerable part of their length (Stensiö, 1937; Gross, 1937; Romer, 1964; Schaeffer, 1981).

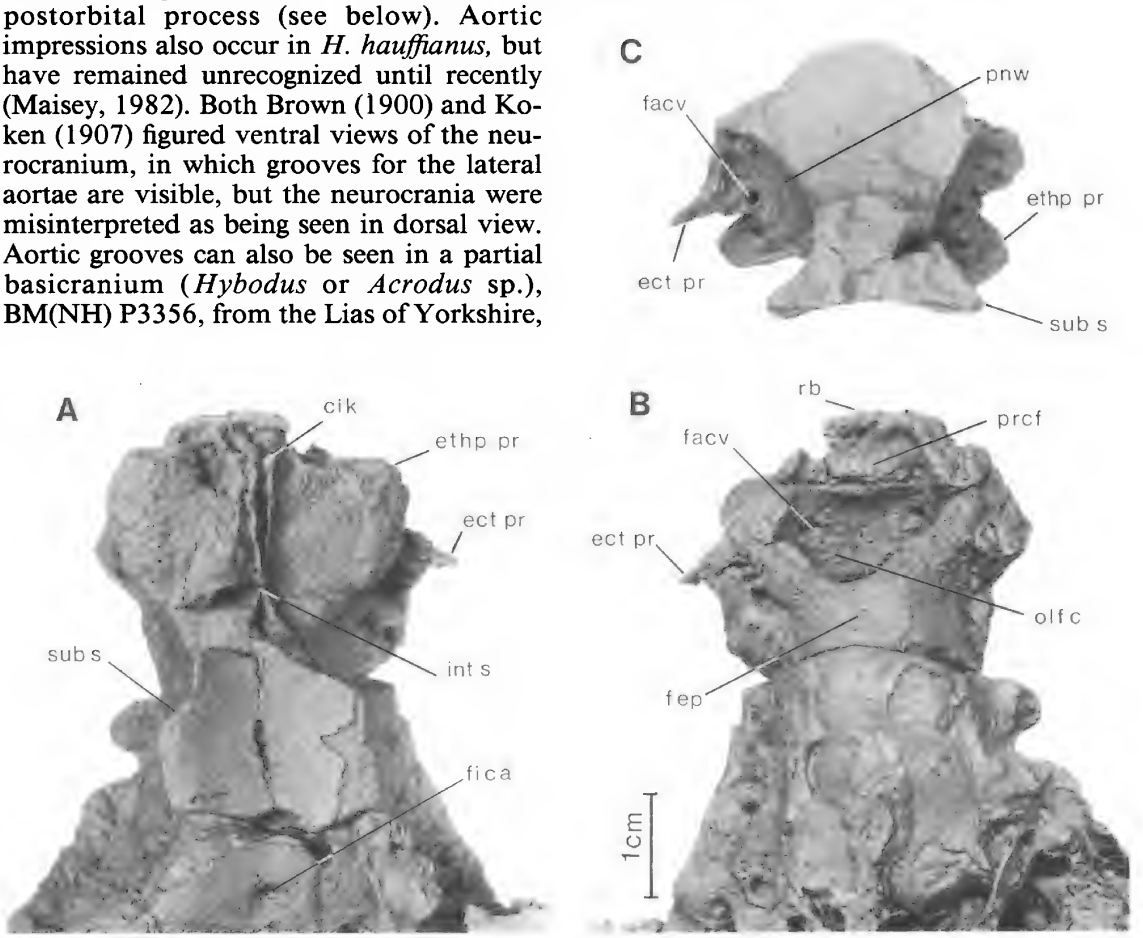


FIG. 10. Anterior part of braincase in BM(NH) 40718, shown in (a) ventral; (b) transverse; and (c) dorsal views. (b) is a somewhat oblique natural break across the mid-orbital region, and is a view looking anteriorly onto the postnasal wall.

Returning for a moment to the imaginary concept of *Hybodus* having a "telescoped" *Xenacanthus*-like neurocranium (see General Features section), it is interesting that in *Xenacanthus* the restored basicranial circulation pattern (Schaeffer, 1981, fig. 12) anterior to the long canals for the lateral aortae is remarkably similar to the entire basicranial circulation pattern of *H. basanus* (fig. 25A). The short bridges under which the lateral aortae pass in *H. basanus* correspond to the much longer aortic canals of *Xenacanthus*. Consequently the impression that "more" of the basicranial arterial complex is uncovered in *Hybodus* than in *Xenacanthus* is illusory. The observed differences in the lengths of enclosed aortae seem to be related only to the greater length of the otic region in *Xenacanthus*.

The orbital artery of *H. basanus* seems to have passed through the suborbital shelf via a short canal located toward the back of the orbit (fora, figs. 3B, 4B, 9B). In this respect *H. basanus* resembles "*Cladodus*" (Stensiö, 1937; Gross, 1937), *Cladoselache* (Harris, 1938), *Tamiobatis* (Romer, 1964; Schaeffer, 1981), *Tristychius* (Dick, 1978), *Xenacanthus* (Schaeffer, 1981), and many modern sharks in which the suborbital shelf is well developed (Holmgren, 1942). DeBeer (1931) showed that in *Scyliorhinus* embryos there are separate blastemic areas lateral to the trabeculae in the neighborhood of the prootic foramen. These blastemas form the subocular cartilage, which wraps around the orbital artery and joins with the lateral margins of the trabeculae, forming subocular shelves. The foramen for the orbital artery in *Scyliorhinus* thus lies at the junction of trabecular and subocular cartilage. Although we have no direct embryological evidence in the case of *H. basanus*, it is reasonable to infer a similar origin for its orbital foramen, as Schaeffer (1981) did in *Xenacanthus, Tamiobatis,* and "*Cladodus.*"

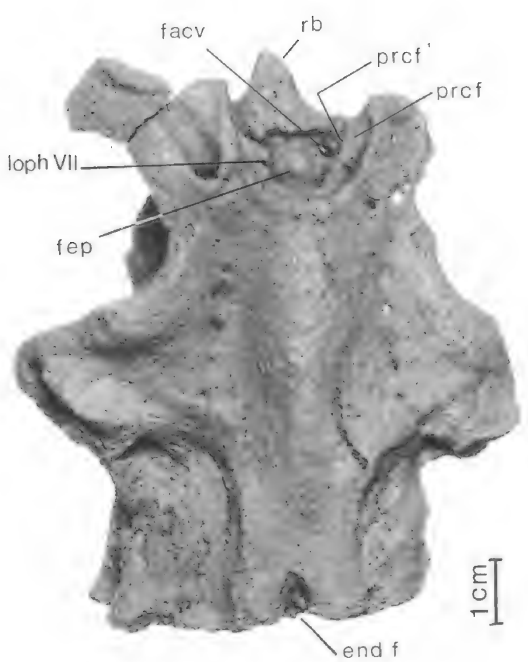


FIG. 11. *Xenacanthus* sp., UM 16194, dorsal view of braincase, Permian, Texas, to show rostral bar, epiphyseal notch and foramina thought to be for the anterior cerebral vein and for a possible medial branch of the lateral ophthalmic ramus (loph VII).

A small distance anterior to the foramen for the orbital artery is another foramen, also penetrating the suborbital shelf. A comparable foramen is also present in *Xenacanthus* (Schaeffer, 1981), "*Cladodus*" *wildungensis* (Gross, 1937), and *Tristychius* (Dick, 1978). The basicranium of *Tamiobatis* is less well known, and its basicranial circulation is not therefore considered here. Interpretation of the second foramen through the subocular shelf has proven problematical. It is widely considered to be for a branch of the palatine nerve (Gross, 1937; Dick, 1978; Schaeffer, 1981). According to Stensiö (1937), his "*Cladodus*" had its palatine nerve foramen farther lateral and posterior to the canal for the orbital artery. Harris (1938) identified a foramen in *Cladoselache* as the common exit for the orbital artery and palatine nerve. This interpretation leaves the orbital artery still ventral to the suborbital shelf of *Cladoselache* and Harris's view was modified by Schaeffer (1981, fig. 13) to bring *Cladoselache* more in line with other Paleozoic sharks. There is consequently considerable disagreement in the literature over interpretation of these basicranial foramina. Comparison with modern sharks is relatively unhelpful. In several groups the suborbital shelf is pierced by a canal for the orbital artery (e.g., *Hetero-*

dontus, Squatina, orectoloboids, galeoids), but the palatine nerve does not pass through the basal plate (fig. 25B). In squaloids the palatine nerve pierces the basal part of the lateral commissure (except in *Oxynotus*) but in virtually all of them the orbital artery does not pass through the suborbital shelf; *Deania* (*Acanthidium*) and *Centroscymnus* are the only genera examined by Holmgren (1941) in which foramina for both the orbital artery and the palatine nerve are present in the basicranium. In hexanchoids and *Chlamydoselachus* neither the orbital artery nor the palatine nerve penetrates the basicranial cartilage (fig. 25C). It is consequently very uncertain that the "extra" foramen in the suborbital shelf of *Hybodus* and *Xenacanthus* contained a branch of the palatine nerve, although such an interpretation may be correct.

Postorbital Process

The postorbital process (po pr) of *H. basanus* is a very prominent feature of the neurocranium. The process is attached to the lateral wall of the otic capsule. In BM(NH) 40718, both postorbital processes became detached during preparation, exposing the otic capsular wall (see also Woodward, 1919, pl. 26, figs. 3, 3A). The right process is missing in figure 3. Interestingly, in other species of *Hybodus* the neurocranium is sometimes preserved with these processes missing, e.g., in specimens of *H. hauffianus* studied by Brown (1900) and Koken (1907). This suggests that attachment of the processes to the otic region was generally quite weak (Maisey, 1982).

The postorbital process is strongly downturned distally (figs. 3C, 6B, 9C–E, 13A, 14A). Its dorsal surface is convex anteroposteriorly, except at a large posterior embayment where the jugular canal emerges. A shallow groove extends from the jugular canal, over the posterolateral surface of the otic capsule, possibly indicating the positions of the lateral head vein (=jugular vein) and/or hyomandibular nerve. This groove is visible in BM(NH) 40718 because the lateral otic process, which would normally obscure it, has been eroded away (fig. 3D); in P60110 this process is present (lot pr) and the groove is obscured (fig. 4C). The postorbital process is somewhat concave ventrally but bulges outward anteriorly. Distally its ventrolateral margin is raised into a narrow plateau which (with jaws in place) lies immediately above the front of the adductor fossa of the palatoquadrate (see below and fig. 16). There are some foramina penetrating the floor of the postorbital process. The largest of these, in the floor of the jugular canal, is crescent-shaped (feha, figs. 3B, 4B, 9B). It possibly housed the palatine nerve, arising from the hyomandibular nerve within the jugular canal. It may have provided a mandibular or hyoid vein with access to the lateral head vein within the jugular canal. Dick (1978) suggested that a mandibular vein penetrated the postorbital process of *Tristychius,* but such a condition does not occur in modern elasmobranchs (Holmgren, 1940, 1943). Another equally unique explanation for this foramen, alluded to earlier, is that it permitted the efferent hyoidean artery to reach the lateral aortae from its origin in the hyoid arch, and/or that it housed the spiracle or spiracular sense organ. Briefly anticipating my description of the hyoid arch, the hyomandibula articulates with the neurocranium immediately behind the postorbital process. The efferent hyoidean artery would either have taken a relatively long route around and under the postorbital process, or else a much shorter route through an opening in the floor of the process. There is no embryological reason to oppose the proposal that the lateral commissure of *H. basanus* was enlarged posteriorly, to such an extent that it partially enclosed the efferent hyoidean artery and spiracular tube, whereas the orientation of the curved fenestra in the floor of the postorbital process suggests that some structure certainly passed anteriorly and ventromedially from the general vicinity of the hyomandibular articulation toward the lateral aorta. Farther forward in the floor of the postorbital process is another smaller opening, which could also be for a branch of the palatine nerve, or for the mandibular nerve.

There is an elongate concave region on the posterolateral surface of the otic capsule of *Hybodus* behind and slightly dorsal to the posterior end of the jugular canal (figs. 2C, 3D). Its length is approximately the same as the articular end of the hyomandibula. In specimens P60110, BM(NH) 40718 and

P11870, the hyomandibular head is close to this position. This depression may therefore represent the articulation between hyomandibula and neurocranium. The lateral head vein would pass from the jugular canal laterally over the hyomandibula, as in living sharks, and dorsal to the vagus nerve as in sharks, dipnoans, and perhaps *Acanthodes* (DeBeer, 1937; Bertmar, 1965; Stensiö, 1969; Jarvik, 1977, 1980).

In P60110 the hyomandibular attachment is overlain by another lateral projection of the neurocranium, essentially separate from the postorbital process (lot pr, fig. 4A, C). Although it is not evident in BM(NH) 40718 (where this part of the braincase has been most damaged by abrasion), some other specimens of *H. basanus* have this additional process. Moreover, there is evidence for it in the specimen of *H. hauffianus* described by Koken (1907) and in *H. fraasi* (Brown, 1900). Anteriorly the margin of the second process is confluent with the posterior dorsal margin of the jugular canal in *H. basanus.* The relationships of this flange to surrounding elements (hyomandibular head, glossopharyngeal nerve, and postorbital process) suggest homology with the lateral otic process of Paleozoic shark neurocrania, e.g., *Tamiobatis, Xenacanthus* (Schaeffer, 1981). This process is discussed further in the following section.

The jugular canal of *Hybodus basanus* is extremely large (jc, fig. 9) and the lateral head vein may have been inflated into a considerable sinus as it left the orbit through the jugular canal. There is disagreement as to whether the lateral head vein actually passed through the so-called jugular canal in various fossil sharks. A canal like that in *H. basanus* is present in "*Cladodus,*" *Tamiobatis, Xenacanthus, Tristychius,* and *Cobelodus* (Stensiö, 1937; Gross, 1937; Romer, 1964; Zangerl and Case, 1976; Dick, 1978; Schaeffer, 1981), and is generally believed to have housed the lateral head vein. Holmgren (1941) suggested that this canal housed the otic ramus of the facial nerve, and that the jugular canal was ventral to the postorbital process in the fossils, as in *Chlamydoselachus.* Comparing the course of the lateral head vein in *Chlamydoselachus* with the large canal in the postorbital process of *Xenacanthus, Tamiobatis,* and "*Cladodus*" *wildungensis,* Schaeffer (1981, p. 20) concluded that there is "no other obvious course for the head vein except through the canal in the postorbital process." I concur with this view, as far as *H. basanus* is concerned, because of the arrangement of the palatoquadrates beneath the postorbital process; there is no room for such a major structure as the lateral head vein between the postorbital process and palatoquadrate. More significantly, however, in *Squatina* the lateral head vein and hyomandibular nerve pass through a canal like that of the fossils, while the otic ramus of the facial nerve can be traced from the infraorbital sensory canal, just anterior to the supraoccipital canal, past the orbital process of the palatoquadrate, to the main trunk of the facial nerve. In *Squatina,* therefore, the otic branch passes through the fossa for the palatoquadrate orbital process. Interestingly, Gegenbaur (1872) termed this fossa the *canalis oticus,* but did not comment on what nerves it contained. According to Holmgren's (1941) hypothesis, the large canals in the postorbital processes of "*Cladodus*" and *Squatina* are not homologous, since according to him the canal of "*Cladodus*" contained the otic branch of the facial nerve, but in *Squatina* it contains the lateral head vein and hyomandibular nerve. Instead, we should have to suppose that the otic canal (="Schaedellucke fur den *Processus palatobasalis*"; Iselstoger, 1937) of *Squatina* is the modern counterpart of the canal through the postorbital process of "*Cladodus*" (and also, presumably, of *H. basanus, Xenacanthus, Tamiobatis, Tristychius,* and *Cobelodus*). Although such an argument cannot be totally refuted by the evidence at hand, it is rejected on the grounds that a far simpler explanation is possible; a jugular canal like that of *Squatina* was indeed present in the fossils just mentioned.

In *H. basanus* there is evidence that the hyomandibular nerve emerged anterior to the postorbital process (hym VII, figs. 13, 14), rather than behind it as in "*Cladodus*" (Gross, 1937) and *Xenacanthus* (Schaeffer, 1981). This may be due to the different relationship between the lateral wall of the otic capsule and the postorbital process in *H. basanus.* The combined trunks of the facial and trigeminal nerves of sharks are anteriorly po-

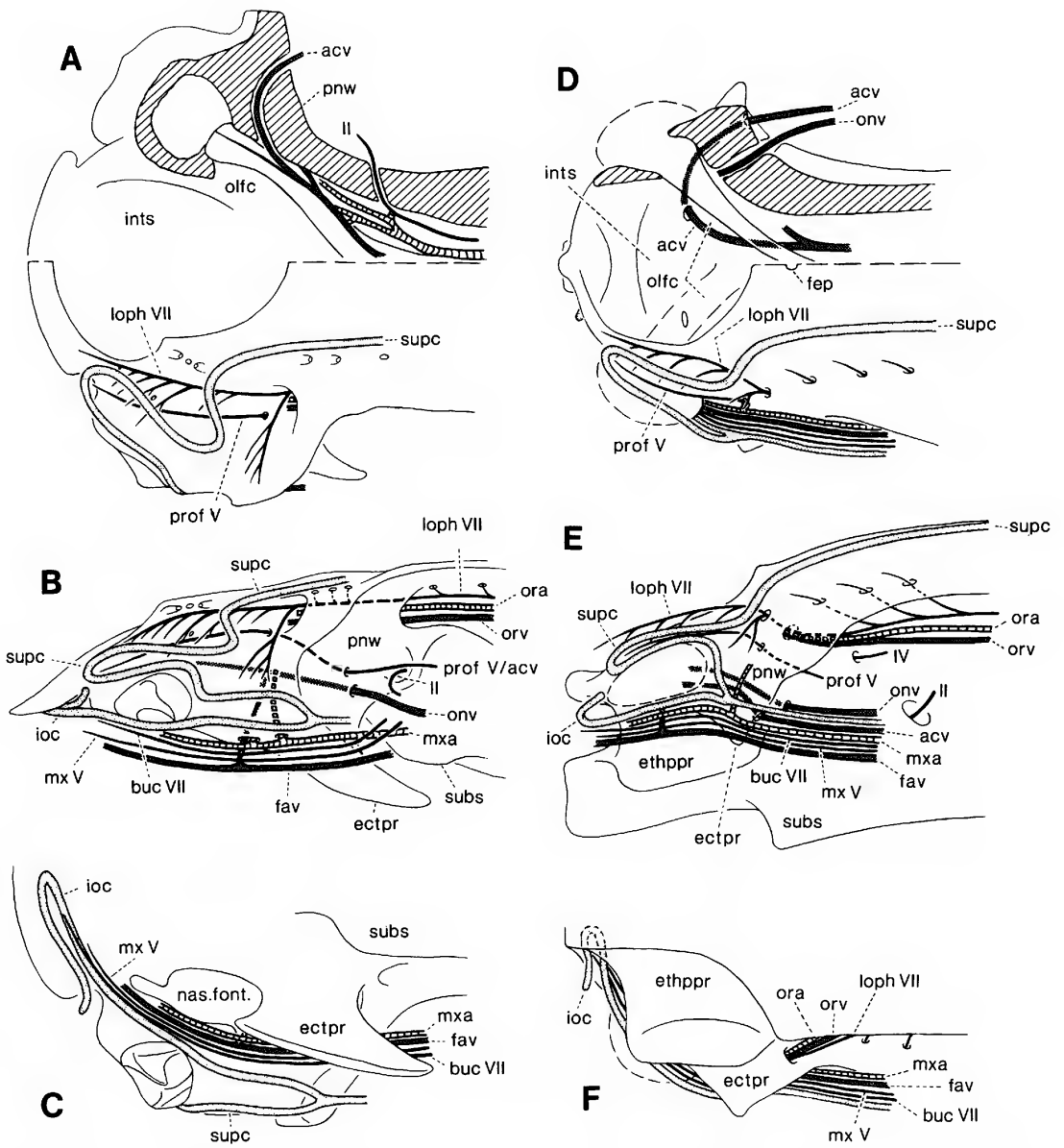


FIG. 12. Ethmoid regions of (a–c) *Chlamydoselachus* (after Jarvik, 1942), and (d–f) *Hybodus basanus* with principal nerves and blood vessels shown schematically. Arrangement in *Hybodus* hypothetical; see text for discussion and justification.

sitioned, relative to the otic capsules, and the hyomandibular branch of the facial nerve initially passes lateral and anterior to the capsular wall. The hyomandibular nerve may emerge from the braincase via a separate foramen (e.g., hexanchoids, *Chlamydoselachus,* most squaloids, *Squatina, Heterodontus,* and batoids). The cartilage separating the hyomandibular nerve from the rest of the facial nerve is the prefacial commissure (Holmgren, 1940) and is not part of the otic capsule. By analogy with modern sharks, the prefacial commissure was extensive in fossils such as "*Cladodus*" and *Xenacanthus* (Schaef-

fer, 1981). In *H. basanus* the prefacial commissure is narrow and the hyomandibular nerve emerged from the braincase before passing through the jugular canal as in *Squatina.* If the hyomandibular nerve of *H. basanus* was to emerge posterior to the postorbital process, as in *Xenacanthus* and "*Cladodus,*" the nerve would have to penetrate the lateral wall of the otic capsule.

Among modern elasmobranchs in which a prefacial commissure is present, the hyomandibular nerve either emerges posterior to the postorbital process (hexanchoids, *Chlamydoselachus,* squaloids), or anterior to it (*Heterodontus,* batoids, *Squatina*). If the latter condition is derived, as its somewhat limited distribution suggests, it may represent a synapomorphy of some or all these forms (including *Hybodus*). As far as *H. basanus* is concerned, however, narrowing of the prefacial commissure seems to be related to the anterior shift of the otic capsules; the lateral commissure has not been affected in the same way. In modern sharks, where the prefacial commissure is entirely within the orbit, the postorbital process is never very extensive anteroposteriorly. Thus, in these modern forms, either both the prefacial and lateral commissures have become narrowed (e.g., *Squatina*) or else the lateral commissure has narrowed, whereas the prefacial commissure has remained long (e.g., *Squalus*). Neither condition corresponds exactly to that found in *H. basanus,* and it is concluded that any similarity between *H. basanus* and modern sharks in this respect has arisen independently.

In only one group of modern sharks (carcharhinids) is the postorbital process located on the lateral wall of the otic capsule. As in other galeoids, however, carcharhinids lack a separate hyomandibular nerve foramen and prefacial commissure. In carcharhinids the palatoquadrate levator muscles have invaded the orbit, from which the eye is effectively displaced. A more primitive state of this condition is found in *Triakis* (Nakaya, 1975); in this form, the levator muscles have invaded the orbital margins, but the postorbital process and supraorbital shelves are well developed. Moreover, the postorbital process of *Triakis* lies essentially anterior to the otic capsules. It is generally accepted that carcharhinids are derived members of the galeomorph group (Compagno, 1973, 1977). There is no evidence in *H. basanus* to suggest that palatoquadrate levator muscles had invaded the orbit. Conversely, the extent of the supraorbital and suborbital shelves, size of the postorbital process, and relationship between this process and the palatoquadrate, all make it extremely improbable that the palatoquadrate levators were at all well developed (see below). Therefore any similarity in the position of the postorbital process in carcharhinids and *H. basanus* is regarded as coincidental and not phylogenetically significant.

Otico-Occipital Region

i. General Features: Woodward (1919, pl. 26, figs. 3, 3A) figured the dorsal and posterior aspects of an incomplete *H. basanus* neurocranium, BM(NH) P13094. Comparison of this specimen with P60110 (figs. 4, 5) shows that the otic region of P13094 is nearly complete, despite the absence of a postorbital and lateral otic process, and the general lack of preparation. The otico-occipital region of BM(NH) 40718 has been heavily eroded, and cleaning the specimen reveals many internal details of the otic region, but very little of its external morphology (fig. 3). The gross morphology of the otico-occipital region in *H. basanus* is as follows. The paired otic capsules take up approximately a third of the total cranial length, and lie close together between the postorbital processes, as discussed earlier (ot cap, fig. 5). The capsules are slightly elongated anteroposteriorly, and between them there is an elongate parietal (endolymphatic) fossa (end f, figs. 2, 9), which extends posteriorly as far as a short median occipital crest. The occipital arch between the parietal fossa and foramen magnum is short. There is no trace of a dorsal otico-occipital fissure of the type Schaeffer (1981) described in *Xenacanthus* and *Tamiobatis.* A large occipital cotylus is preserved in only a few specimens of *H. basanus,* including BM(NH) 40718, P3172c, P60110, and P13094. The cotylus (oc cot, figs. 4, 5) is almost circular, but is drawn out on each side, thus adding some lateral support to the spino-occipital joint. A large glossopharyngeal-vagus fossa is present

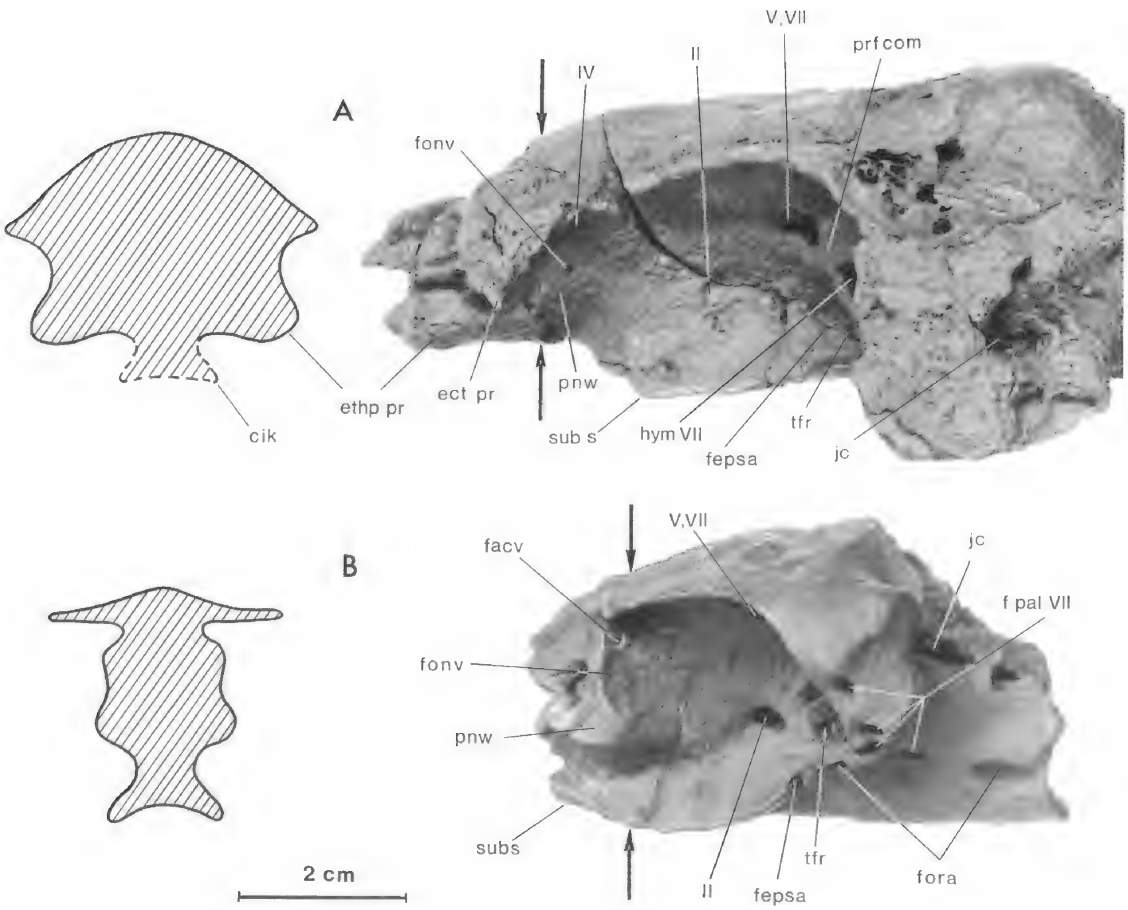


FIG. 13. Left orbits of (a) *Hybodus basanus,* BM(NH) 40718 and (b) *Xenacanthus* sp., PU 22391B, Permian, Texas, with principal foramina identified. Trigeminofacialis recess of *Hybodus* is visible in lateral view, but is obscured in *Xenacanthus* by the postorbital process. Sections to left of photographs are diagrammatic, but are based on sections through casts of originals, immediately behind the precerebral fontanelle as indicated on the photographs.

on each side of the foramen magnum, just behind the hyomandibular articulation, and below the posterior vertical canal of the otic capsule (IX, X, figs. 4A, 5). The occiput projects well beyond the posterior border of the otic capsules as in *Xenacanthus, Tamiobatis, Tristychius, Cladoselache,* and *Cobelodus* (fig. 15), whereas in modern elasmobranchs the occiput is situated between the otic capsules, so that the lateral otic process (where present) and glossopharyngeal foramen are more lateral to the occiput than in the fossil genera (Schaeffer, 1981). In modern elasmobranchs (fig. 15A) the fused occipital arches and first vertebral demi-centrum become enclosed on either side by the auditory capsules (DeBeer, 1937), as a result of which the spino-occipital nerves leave the braincase either with the vagus nerve or at a level which falls behind the condyles (Norris and Hughes, 1920). In *Xenacanthus* and *Tamiobatis* (fig. 15) the occipital region projects behind the auditory capsules (Schaeffer, 1981), as it does (albeit to a lesser extent) in *Hybodus* (fig. 15C). Although foreshortened in comparison with these Paleozoic shark braincases, the otico-occipital

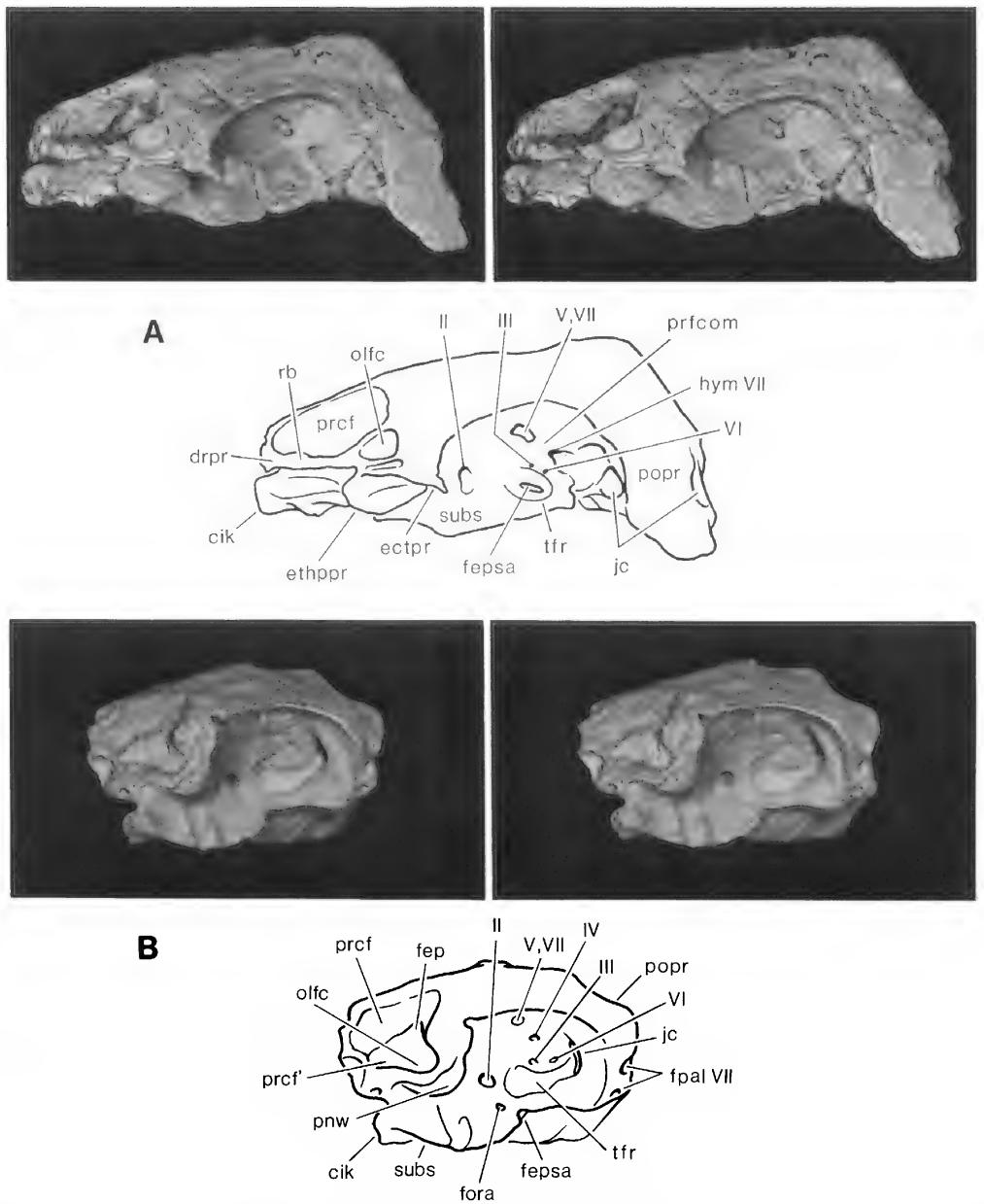


FIG. 14. Stereo-pairs of the braincase of (a) *Hybodus basanus*, BM(NH) 40718 and (b) *Xenacanthus* sp., PU 22391B. Both views are somewhat oblique to show features within the orbit that would be concealed in lateral view. Important features of the ethmoid and orbital region are indicated on the key diagrams. Note inturned cartilaginous margin to precerebral fontanelle and epiphyseal notch in *Xenacanthus* (seen also in fig. 11).

region of *Hybodus* resembles their condition more than the neoselachian one. Schaeffer's (1981, p. 60) proposal that the position of the occipital arch between the auditory capsules is a selachian synapomorphy is not refuted by *H. basanus*.

ii. ENDOLYMPHATIC (PARIETAL) FOSSA: There are thin paired vertical laminae of pris-

matically calcified cartilage, deep within the parietal fossa of *H. basanus* (fig. 3A). These laminae, only visible in sufficiently excavated specimens [e.g., BM(NH) 40718, P13094] probably represent the poorly calcified medial walls of the otic capsules. AMNH 4692 was sliced transversely through the postorbital process. The sectioned surfaces show thin medial walls of the otic capsules and also a thin calcified synotic tectum, deep within the parietal fossa. Traces of this tectum are also visible in the excavated parietal fossa of BM(NH) 40718. The medial walls of the otic capsules were apparently uncalcified for part of their length. In living sharks, the posterior vertical canal bulges into the region of the parietal fossa where the capsule wall is incomplete (Norris, 1929; DeBeer, 1931). The same problems of interpretation attend this region in *H. basanus* as they do in *Xenacanthus* (Schaeffer, 1981). Unlike in *Xenacanthus,* the posterior border of the parietal fossa in *H. basanus* is not extended posterolaterally into persistent otico-occipital fissures. Thus in *H. basanus,* as in modern sharks, the embryonic metotic fissure appears to have closed during ontogeny.

Schaeffer (1981) regarded the presence of the metotic fissure in adult *Xenacanthus* and *Tamiobatis* neurocrania as a synapomorphy. According to Zangerl (personal commun. and in preparation) this fissure is present in other, apparently unrelated Paleozoic sharks. The metotic fissure is considered in more detail below.

There is little evidence for endolymphatic or perilymphatic apertures and canals in *H. basanus.* Part of a small calcified canal is preserved in BM(NH) 40718 (fig. 3A), just medial to the right anterior semicircular canal (asc), and may represent the anterior limit of an endolymphatic passage which originally entered the otic capsule farther posteriorly. This suggests that rather more of the endolymphatic system was contained within the braincase roof of *H. basanus* than in modern elasmobranchs. Alternatively, the canal fragment may have formed part of the acousticolateralis system of the head, but it seems too far removed from the other canals for this to be the case. As in *Xenacanthus* (Schaeffer, 1981) incomplete calcification in *H. basanus* makes impossible the detailed study of the relationship of the perilymphatic fenestra to the posterior semicircular canal, and between the perilymphatic and endolymphatic openings. Nevertheless, in BM(NH) 6356 paired epaxial muscle fibers are preserved, overlying the dorsal surfaces of the otic capsules (figs. 21, 22). Similar epaxial muscle extends anteriorly on either side of the parietal fossa in modern elasmobranchs, and slips of this muscle are directed into the parietal fossa and attach to the endolymphatic pouches (Norris, 1929; Marinelli and Strenger, 1959). Schaeffer (1981) suggested that similar epaxial muscle extended from the dorsal otic ridges of *Xenacanthus, Tamiobatis,* and "*Cladodus.*"

iii. THE AUDITORY CAPSULES: Preservation of BM(NH) 40718 is such that the anterior ampullae of the horizontal and anterior vertical semicircular canals are hollow voids, although the large saccular-utricular cavities have become filled by matrix (fig. 3A). The course of the semicircular canals may be interpreted from exposed portions of their calcified walls in this specimen.

The sacculus lies below and is surrounded by the three semicircular canals. The anterior vertical canal (asc, fig. 3A) is the shortest with its distal ampulla rising next to the utriculus. The canal passes obliquely back toward the midline before plunging deeper toward the sacculus. The horizontal canal (hsc) arises lateral to the utriculus, then curves laterally around the sacculus until it turns mesially again above the exits for the vagus nerve. The posterior vertical canal (psc) is the least evident from BM(NH) 40718, and is visible only where the endolymphatic fossa has been excavated. Its position is marked by a ridge in BM(NH) P60110 (fig. 4A).

iv. THE VAGUS-GLOSSOPHARYNGEAL FOSSA: In *Hybodus basanus* there is a broad fossa on either side of the *foramen magnum* (figs. 3A, 5, 8E, 9E). Each fossa is located just behind the hyomandibular articulation and below the posterior vertical canal of the auditory region. In modern elasmobranchs the vagus nerve leaves the neurocranium in this position. The vagus nerve of *H. basanus* probably occupied the fossa, perhaps along with the glossopharyngeal nerve, some spinooccipital nerves and the posterior cerebral vein. One specimen figured by Woodward (1919, pl. 26, figs. 3, 3A), BM(NH) P13094,

is inadequately prepared and a large part of the "floor" of the vagus-glossopharyngeal fossa is actually matrix. In BM(NH) 40718 the fossa is floored by a cartilaginous lamina which extends laterally beneath the otic capsule and which is interpreted as a hypotic lamina. In *Scyliorhinus* the hypotic lamina extends laterally from the embryonic parachordal cartilage beneath the posterior part of the otic capsule (DeBeer, 1931), although the floor of the capsule may not be calcified. In *Squalus,* however, the capsule floor is calcified (El-Toubi, 1949). *Hybodus basanus* seems to correspond to this condition more closely than to the one in *Scyliorhinus.* Neither *Squalus* nor *Scyliorhinus* has a fossa for both the vagus and glossopharyngeal nerves. A vagus-glossopharyngeal fossa is present in *Chlamydoselachus* (Allis, 1923). More usually, the exits for the vagus and glossopharyngeal nerves are separated by the posterior semicircular canal, which in modern elasmobranchs lies between the passages for these nerves (Schaeffer, 1981). In *Chlamydoselachus,* and apparently also in *Hybodus,* the posterior part of the otic region is modified so that the vagus fossa is expanded beneath the otic capsule to become confluent with the glossopharyngeal foramen. In *Heterodontus* there is a shallow vagus fossa, lateral to the foramen magnum, but the fossa is clearly separated from the glossopharyngeal foramen (Daniel, 1915), as in the majority of living elasmobranchs. In *Xenacanthus* the courses of the glossopharyngeal and vagus nerves are somewhat uncertain, but they presumably lay somewhere within the otico-occipital (metotic) fissure, which is persistent into adulthood (Schaeffer, 1981). The metotic fissure of developing *Scyliorhinus* becomes closed during ontogeny, apart from passages from the glossopharyngeal and vagus nerves (DeBeer, 1931). It is concluded that a similar developmental pattern to this occurred in *H. basanus* since the specimens examined [e.g., BM(NH) 40718, P13094] are comparatively small ones, yet have no indication of a persistent otico-occipital fissure.

In the present context, fusion of the hypotic lamina with the otic capsular floor (and the consequent formation of glossopharyngeal and vagus canals) is regarded as a derived condition uniting modern sharks with *Hybodus, Palaeospinax* (Maisey, in preparation), a Permian "Euselachian" (Schaumberg, in preparation) and *Tristychius* (Dick, 1978).

v. The Lateral Otic Process: In *Hybodus basanus* the lateral wall of the otic capsule is overlain by a broad flangelike process (lot pr, figs. 4, 5). The relationship of this process to surrounding structures, such as the otic capsules, the hyomandibular articulation (located ventral to this process), and the presumed course of the lateral head vein and glossopharyngeal nerve, all suggest that the process corresponds to the lateral otic process (Romer, 1964) of *Tamiobatis* and *Xenacanthus,* although it is clearly impossible to establish homology by means of embryological studies.

In *Tamiobatis* and *Xenacanthus* the posterolateral wall of the otic capsule is overlain by the lateral otic process (Romer, 1964), upon which the hyomandibular articulation is partly situated (Schaeffer, 1981), lateral to the ventral otic notch which probably housed the glossopharyngeal nerve. A comparable process is generally poorly developed in modern elasmobranchs; e.g., the "post-otic" process (Holmgren, 1941) of *Squalus, Centrophorus,* and *Deania* (*Acanthidium*) and the "Haifortsatz" of *Squatina* (Iselstoger, 1937). In *Squatina* and *Squalus* this process contains the glossopharyngeal foramen and contributes ventrally to the hyomandibular articulation (Iselstoger, 1937; Schaeffer, 1981). The glossopharyngeal foramen apparently differs from the "post-otic" foramen of Holmgren (1941), which he states is absent in forms such as *Squatina,* his "*Scymnorhinus*-type" squaloids, *Chlamydoselachus, Heterodontus,* chiloscyllids, *Orectolobus,* and "galeoids." Thus he found sharks with both a "post-otic" process and foramen ("*Squalus*-type" squaloids) and others in which the process is present but not the foramen (e.g., *Squatina, Mustelus*).

In many batoids (e.g., rhinobatids, *Raja, Pristis*) there is a cartilaginous bridge joining the posterior corner of the basal plate with the lateral wall of the otic capsule. This bridge is located dorsal to both the glossopharyngeal nerve and lateral head vein (Holmgren, 1941). Unfortunately the embryonic development of these processes has not been adequately

studied in living elasmobranchs. According to Holmgren (1940, p. 188), the cartilaginous bridge in batoids is of visceral arch origin; he regarded it as forming from a mesenchymatous pharyngohyal blastema, in conjunction with the hyomandibular articulation, and he believed this to be a different situation from sharks (Holmgren, 1940, 1943, p. 75). Jollie (1971) found evidence that in *Squalus* both the articular area of the hyomandibula and the *lamina hypotica* are formed, as in batoids, from the blastemic upper end of the hyoid arch. Neither Holmgren (1940, 1941, 1943) nor Jollie (1971) discussed the origin of the "post-otic process" or post-otic foramen in squaloids, however. The process is shown in 59 mm. *Squalus* embryos by Holmgren (1941, figs. 76, 78), in 35–37 mm. *Squalus* by Jollie (1971, fig. 7), and in 43 mm. and larger *Etmopterus* embryos by Holmgren

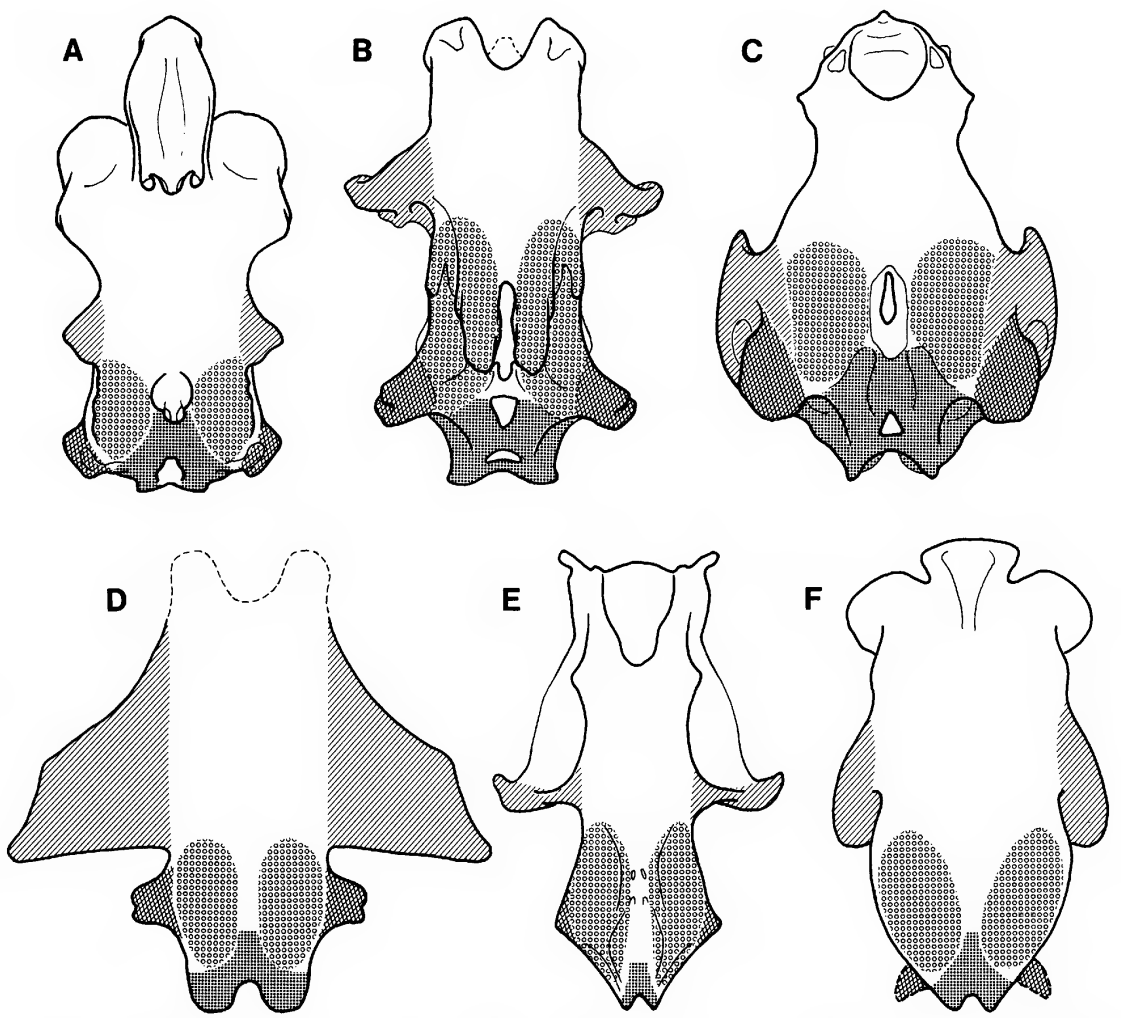


FIG. 15. Dorsal views of the braincase in (a) *Squalus*; (b) *Tamiobatis* (after Schaeffer, 1981); (c) *Hybodus basanus*; (d) *Cladoselache* (after Harris, 1938); (e) *Tristychius* (after Dick, 1978); and (f) *Cobelodus* (after Zangerl and Case, 1976, with addition of lateral otic processes as in *Symmorium*). Key as follows: diagonal lines = postorbital process, cross-hatching = lateral otic process, open circles = otic capsules, stipple = occipital arch and cotylus. Arrangements of these structures are similar in (b); (d); (e); and (f); (a) differs in the position of the occipital arch; (c) differs in the position of the postorbital process; otherwise (a) and (c) resemble the other forms.

(1940, figs. 89–91, 96, 97). At earlier stages the process seems to be absent and it is concluded that development of the "post-otic process" occurs relatively late in ontogeny. Holmgren (1940, p. 140) noted that in 43 mm. *Etmopterus* embryos the fate of the mesenchymatous "pharyngohyal" is uncertain, and that parts of it may have become plastered to the lateral wall of the otic capsule.

Development of the head in *Squatina* is unknown, and it is consequently not possible to determine the origin of the "Haifortsatz" in this elasmobranch. Nevertheless, the intimate association of this process with both the hyomandibular articulation and the glossopharyngeal canal (which is presumably floored by part of the hypotic lamina, as in other elasmobranchs) suggests that it is derived, at least in part, from the same blastemic tissue as in other elasmobranchs, perhaps from that forming the upper end of the hyoid arch. Equally plausibly, the lateral otic process of *Xenacanthus, Tamiobatis,* and *Hybodus* was also formed in this way. It is therefore concluded, albeit very tentatively, that the process under discussion is homologous in all the forms discussed here. Clearly there are important differences, such as whether the glossopharyngeal nerve passes through or just behind the process, and whether or not a post-otic foramen is present. The extent to which the lateral otic process is developed therefore varies among modern and fossil sharks and rays, and its significance is as yet poorly understood. Schaeffer (1981) noted that in modern sharks the hyomandibular articulation is consistently just anterior to the glossopharyngeal foramen, although in *Xenacanthus* and *Tamiobatis* the persistent metotic fissure makes it difficult to locate the original position of the glossopharyngeal nerve. A post-otic foramen was not noted in *Xenacanthus* or *Tamiobatis* by Schaeffer (1981).

As interpreted by Dick (1978), the hyomandibula of *Tristychius* articulated with the neurocranium a considerable distance anterior to both the glossopharyngeal foramen and the lateral otic process. The lateral otic process of *Tristychius* would, in that case, probably not be formed by condensation from a mesenchymatous upper part of the hyoid arch blastema, since it would lie too far posteriorly. Although embryological data concerning development of the selachian lateral otic process are incomplete, observations of the consistent arrangement of the hyomandibular articulation, glossopharyngeal foramen and lateral otic process in fossil and modern sharks suggest either that (a) *Tristychius* is autapomorphic in its hyomandibular arrangement, and its neurocranial otic process is different from the lateral otic process of other sharks, or that (b) its hyomandibular articulation actually lay farther posteriorly, ventral to the lateral otic process and immediately anterior to the glossopharyngeal foramen.

vi. THE OCCIPUT: Between the vagus-glossopharyngeal fossa and the occipital cotylus of *H. basanus* are two or three external foramina, presumably for spino-occipital nerves (fson, fig. 9C). A single foramen, located lateral to the cotylus of the Liassic hybodontid, BM(NH) P50869, corresponds topographically to the posteriormost one in *H. basanus.* In BM(NH) P50869 there are six ventral spino-occipital openings in the inner wall of the chordal canal. This is a remarkably large number of spino-occipital nerves for a neurocranium with such a short occipital region; even xenacanths only seem to have three (Schaeffer, 1981, figs. 6, 14). The internal arrangement of these foramina and those of the vagus, glossopharyngeal, and acoustic nerves is very similar to that in *Hexanchus* (Gegenbaur, 1872, pl. 4, fig. 2; Maisey, in preparation). Although *H. basanus* may have fewer spino-occipital nerves than the Liassic hybodontid, it is possible that some of these nerves combined in *H. basanus* before leaving the occiput via common exits. At least one of the foramina in *H. basanus* seems high enough, relative to the *foramen magnum,* to represent a dorsal spino-occipital foramen. The number and arrangement of spino-occipital nerves is unknown in *Tamiobatis,* "*Cladodus,*" *Cladoselache,* and *Cobelodus.* According to Dick (1978) there are two ventral spino-occipital foramina in *Tristychius.*

Calcified vertebral centra are absent in hybodontids, which apparently retain an unconstricted notochord. It is therefore nonsensical to regard the occipital cotylus of *H. basanus* as an anterior half-centrum which

has become incorporated into the neurocranium between the otic capsules, as in modern sharks and the late Jurassic *Protospinax* (Maisey, 1976). Nonetheless, the notochordal entry into the occiput, in the center of the cotylus, is extremely small and could justifiably be termed a constriction. Verification of this comes from the Liassic hybodont, BM(NH) P50869, in which the notochordal space in the basicranium is broken through and seems to be larger than the diameter of the opening in the cotylus. The extent of the notochord in the basicranium of other fossil sharks is unknown.

The Significance of "Long" and "Short" Otic Regions

Schaeffer (1981, p. 60) suggested that all sharks are united by the location of the occipital arch anteriorly between the auditory capsules, a condition which is otherwise found only among certain actinopterygians. This apomorphic condition is most evident in modern sharks and rays, *Hybodus, Xenacanthus,* and (to a lesser extent) *Tamiobatis*; i.e., those sharks known (apart from *Tamiobatis*) to have elasmobranch gill arch morphology as defined by Nelson (1969). Although Schaeffer (1981) speculated that other sharks may have had a similarly-positioned occipital arch (e.g., *Tristychius, Cobelodus, Cladoselache*), in none of these forms can this condition have been so well developed as in modern sharks, *Hybodus* and *Xenacanthus* (fig. 15). In *Tristychius,* however, the slender occipital arch may have extended between the auditory capsules for some distance anteriorly (Dick, 1978). I therefore agree with Schaeffer (1981) that the position of the occipital arch in elasmobranchs (including *Hybodus, Tristychius, Xenacanthus, Tamiobatis, Ctenacanthus,* and modern sharks) is apomorphic, but disagree that this character represents a synapomorphy for all sharks. According to his cladogram (Schaeffer, 1981, fig. 26B) the character is a synapomorphy of chondrichthyans (his character 19a), although there is no evidence that the occipital segment occupies this position in chimaeroids. Furthermore, separate foramina for spino-occipital nerves occur in *Hybodus* and hexanchoids, and in *Hybodus* the occipital arch projects beyond the auditory capsules and is perforated by the spino-occipital foramina which do not open within the glossopharyngeal-vagus fossa (Schaeffer's character 19b, supposedly uniting *Hybodus* with modern sharks).

Hybodus basanus superficially resembles modern sharks, *Cobelodus* and *Cladoselache* in its short otico-occipital region, and contrasts with *Xenacanthus* and *Tamiobatis,* in which this region is more elongate. Schaeffer (1981) has suggested that the longer condition may be derived, but an alternative view (that the longer condition is primitive) is equally plausible. As far as *H. basanus* is concerned, the configuration of its otic capsules, occiput, postorbital process, and lateral otic process (discussed further below) is distinctive, as figure 15C illustrates.

The short otico-occipital region of *Cladoselache* resembles that of modern elasmobranchs in the relative positions of the otic capsule and lateral otic process, which lie essentially posterior to the postorbital process (fig. 15A, D). In this respect, *Cladoselache* and modern elasmobranchs agree with *Xenacanthus, Tamiobatis,* and *Tristychius* (fig. 15B, E). *Cobelodus* also agrees with this arrangement, although lateral otic processes have not been described (fig. 15F). In *H. basanus* the otic capsules are located mesial to the postorbital processes (see earlier discussion). *Hybodus basanus* and modern sharks differ in the location of the occiput relative to the posterior margin of the otic capsules (see above). Simply arguing in terms of commonality, the arrangements of the otic capsules in *H. basanus* and of the occiput in modern elasmobranchs represent separate and distinct apomorphic states. Conversely, the arrangement of the occiput in *H. basanus,* and the otic capsule/postorbital process configuration in modern elasmobranchs both conform to the widespread pattern seen in other fossil sharks, and may therefore be primitive (corroborated by outgroup comparison with *Acanthodes bronni,* sarcopterygians, actinopterygians, and placoderms). Modern sharks and *H. basanus* are therefore regarded as being divergently specialized with respect to their otico-occipital regions. This is corroborated by a Permian "euselachian" from Germany (Schaumberg, personal commun. and in preparation). In view of these

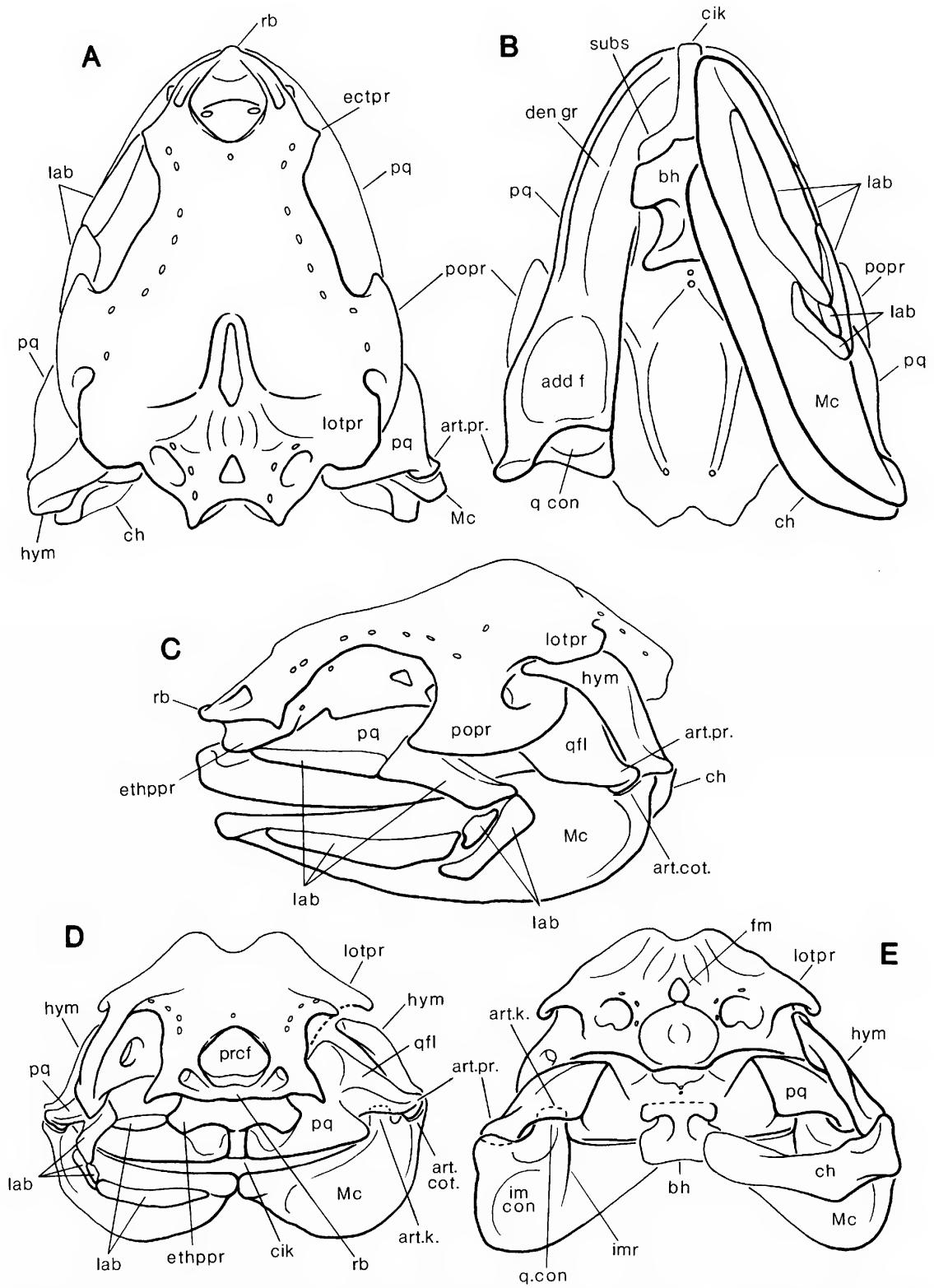


FIG. 16. Restoration of *Hybodus basanus* braincase, jaws, and hyoid arch, in (a) dorsal; (b) ventral; (c) left lateral; (d) anterior; and (e) posterior views. Some elements of mandibular and hyoid arches are omitted on one side.

differences, and also because (a) other "short" Paleozoic shark neurocrania are now known, and (b) the "long" condition may itself be derived (Schaeffer, 1981), the fact that *H. basanus* and modern sharks have a short otico-occipital region does not by itself offer evidence for a relationship between them.

THE VISCERAL SKELETON

General Features

In several specimens of *Hybodus basanus* the visceral skeleton is well preserved, although the posteriormost branchial arches are usually damaged and incomplete. The jaws (palatoquadrates and Meckel's cartilages), labial cartilages, hyomandibula, ceratohyal and basihyal, ceratobranchials, and epibranchials are mineralized perichondrally and are well preserved, but in none of the prepared material is there evidence that the pharyngobranchials, hypobranchials, or basibranchials were perichondrally calcified (figs. 2B, C, 4A, C, 5, 6, 16). These uncalcified parts of the visceral skeleton are consequently unknown in *H. basanus.*

The jaws are longer than the cranium (Woodward, 1916, p. 6) and extremely robust. The jaw-joint lies behind the otic region, not so far back as in *Chlamydoselachus,* but considerably farther back than in *Heterodontus* where the jaw-joint lies below the orbit. Each cheek is supported by massive labial cartilages, comparable in size with postmandibular arch components (figs. 2C, 4C, 6C, E, 16). The hyomandibula (figs. 4D, E, 6C, D) is directed downward, posteriorly and slightly outward. In *Chlamydoselachus* the hyomandibula is directed essentially posteriorly (Allis, 1923), but its distal end is swung out laterally, to broaden the oropharyngeal cavity, as the mouth opens (Smith, 1937). In many other modern sharks, and in *Tristychius* (Dick, 1978), the hyomandibula is directed downward, laterally and even anteriorly. In hexanchoids, *Cladoselache,* and *Xenacanthus* the hyomandibula is oriented more as in *Chlamydoselachus.* Zangerl and Williams (1975) and Zangerl and Case (1976) reconstructed the hyoid arch of *Cobelodus* in the same fashion as *Chlamydoselachus,* except that they considered this arch to be nonsuspensory (aphetothyoidean) in *Cobelodus.*

There is evidence in *H. basanus* and other *Hybodus* species of five branchial arches, as in most modern elasmobranchs. The number of branchial arches in other fossil sharks has generally been uncertain. Dean (1909, p. 218) considered that in *Cladoselache* "they certainly number five on each side, and there may have been a sixth and even a seventh." A cladoselachian from Tennessee (NMNH 20675) clearly has only five branchial arches, however (Maisey, 1980 and in preparation). Zangerl and Case (1976) only found calcified elements of three branchial arches in *Cobelodus,* but suggest that others were present. Dick (1978) restored *Tristychius* with five branchial arches on the basis that in one specimen five ceratobranchials are visible. The number of branchial arches in xenacanths has not been reliably determined. Specimens of *X. decheni* and "*Pleuracanthus*" *oelbergensis* figured by Fritsch (1895, pl. 96, figs. 1, 4) seem to have six arches behind the hyoid, but Jaekel (1906) restored "*P.*" *sessilis* with five.

Labial Cartilages

In *Hybodus basanus* the labial cartilages are enormous, and relative to head size are perhaps the largest of any known shark. Woodward (1916) identified four pairs of labial cartilages in *H. basanus* but BM(NH) 40718 clearly shows five, and other specimens, e.g., BM(NH) P60110 and BM(NH) P13094, AMNH 4692, suggest this is probably more usual (figs. 2B, C, 4C, 6). Woodward's (*ibid.*) "lower anterior" is actually two chondrifications, a longer anterior one and a much smaller posterior one (here termed the articular labial cartilage because it forms the joint between lower and upper elements).

The upper and lower anterior labial cartilages are elongated, but only the lower anterior one rests in a groove (figs. 2B, 4C, 6B, E, 16). The upper one terminates anteriorly beneath the ectethmoid process, and passes obliquely back beneath the orbit and almost reaches the postorbital process. Here it is overlain by the posterior upper labial cartilage, a broad-headed element with a flattened upper and rounded lower cross-section. There is a flat articular surface between this element and the anterior upper labial.

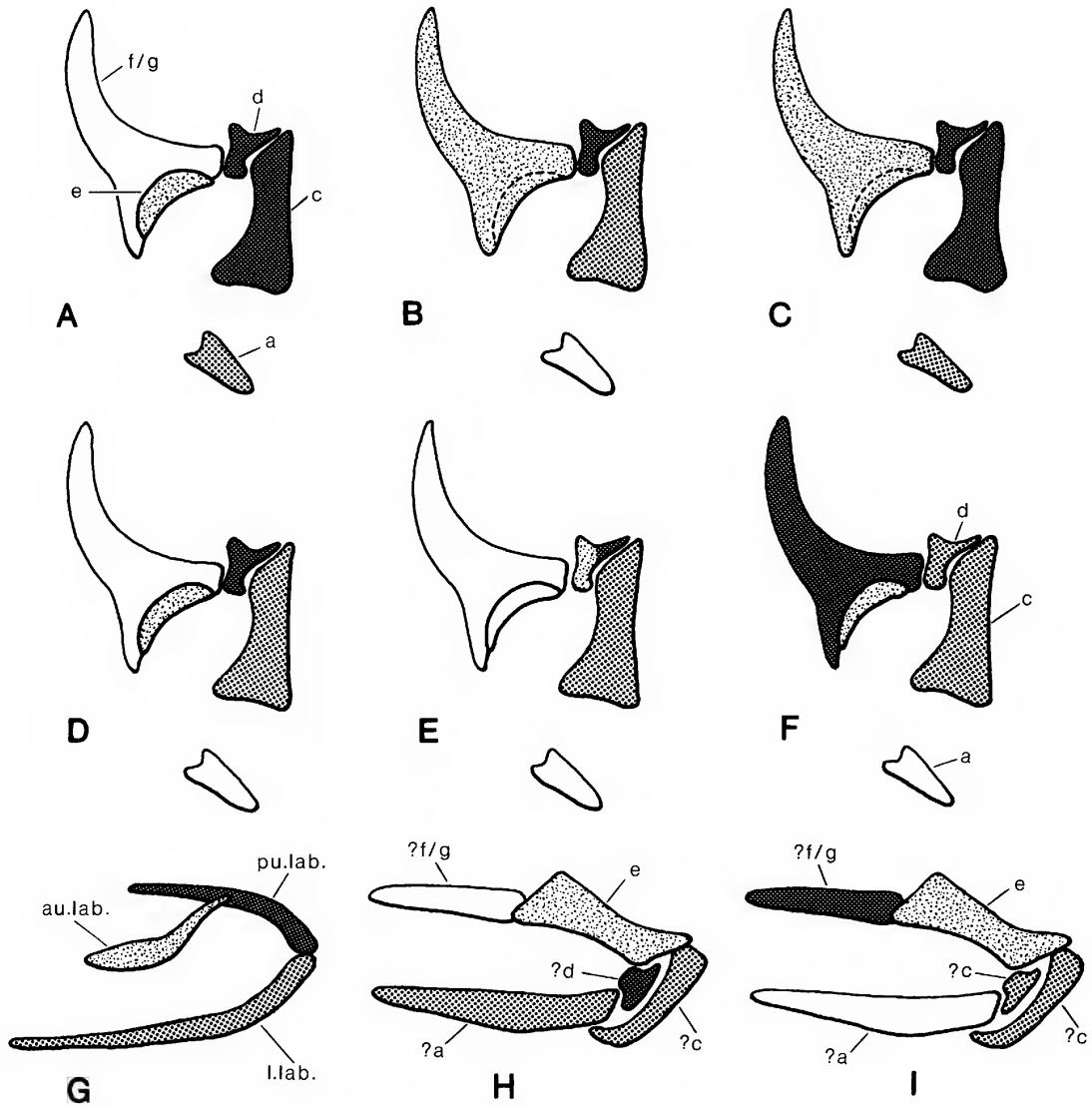


FIG. 17. Labial cartilages of sharks and chimaeras to illustrate various hypotheses of homology. Shading in *Chimaera* and *Hybodus* is keyed to (g). Lettering after Hubrecht (1876). (a–f) *Chimaera,* homology according to (a) Hubrecht, 1876; (b) Vetter, 1878; (c) Luther, 1909; (d) Allis, 1917; (e) Holmgren, 1942; and (f) suggested in text, with no ontogenetic transposition of upper labials; (g) *Chlamydoselachus* (to represent modern elasmobranchs), after Allis, 1923; (h, i) *Hybodus basanus,* two possible interpretations with (h) and without (i) ontogenetic transposition of the upper labials (interpretation of lower labials somewhat arbitrary). Unshaded elements are presumed to lack a homolog in *Chlamydoselachus* labials.

At the joint between upper and lower labials is the small articular cartilage (?d; fig. 17H) omitted by Woodward (1916). This and the posterior lower labial cartilage probably acted as joint fulcra, and articulate with the lower anterior element. As might be expected, the corner of the mouth is adjacent to the labial joint; the position of the oropharyngeal denticles was carefully noted as preparation proceeded, and those lining the mouth terminated near here.

The labial cartilages of *Hybodus basanus* are of interest in several respects. In addition to their considerable size, the labial cartilages

are more numerous than in modern elasmobranchs. Furthermore, the apparent presence of articular surfaces between some of the labial cartilages in *H. basanus* suggests that an intrinsic musculature was well developed. In these respects the labial cartilages of *H. basanus* seem more like those of modern chimaeras than those of modern sharks and rays.

In modern sharks there are at most three labial cartilages per side (fig. 17G), two upper and one lower (Gegenbaur, 1872). There are two pairs in *Notorhynchus* (Daniel, 1934) and one in rhinobatids. In narkids there are three pairs of labial cartilages, but other batoids lack them (Holmgren, 1942). Among fossil chondrichthyans, *Tristychius* appears to have at least two pairs of labial cartilages (Dick, 1978). In *Notorhynchus* the single upper labial cartilage may result from "fusion" of the anterior and posterior elements (Holmgren, 1942), although there is no embryological evidence that this is the case and it is possible that the single element has arisen because one of the two chondrification centers failed to develop in the labial blastema. The anterior upper labial of modern sharks is anterior (oral) and external (lateral) to the posterior upper labial; e.g., *Chlamydoselachus* (Fürbringer, 1903; Luther, 1908; Goodey, 1910; Allis, 1917, 1923), *Mustelus* (Allis, 1917), and *Squalus* (Holmgren, 1940, 1942). Interestingly, the so-called anterior upper labial first develops dorsally and behind the posterior upper labial, and later shifts to its adult position during ontogeny (Holmgren, 1942, p. 246).

According to Holmgren (1942, p. 241 *et seq.*), modern chimaeras possess large superior and inferior maxillary cartilages and also paired premandibular, premaxillary, and prelabial cartilages. This terminology is somewhat unfortunate since there are connotations of homology with dermal bones (e.g., premandibular, prelabial). As Allis (1917) demonstrated, however, the essentially alphabetical terminology of some earlier workers is little better.

Among modern elasmobranchs, labial musculature is generally lacking. A few *M. preorbitalis* fibers are inserted into the upper end of the posterior upper labial cartilage in *Heterodontus,* and insertions may also be present in *Pristiurus, Mitsukurina,* and *Mustelus* (Luther, 1908). According to Moss (1977, p. 361) *Ginglymostoma* labials "have a relatively prominent intrinsic muscle which passes from the posterior face of the ventral cartilage to the posterior face of the intermediate cartilage." The anterior upper labial of *Chlamydoselachus* is strongly attached to the *M. levator labii superioris* by connective tissue, and fibers of the *M. adductor mandibulae* are attached mesially to the middle of the posterior upper labial, whereas the tendon of the *M. protractor anguli oris* and a few fibers of the *M. adductor mandibulae* are attached to the posterior end of this element (Allis, 1923). In chimaeras labial musculature is well developed, with six paired muscles (Luther, 1909; Holmgren, 1942). These muscles can be divided into two groups, according to their innervation, although there is some disagreement in the literature over the innervation of one of the muscles, the *M. levator anguli oris posterior* (cf. Holmgren, 1942, p. 250; Jarvik, 1980, vol. 2, p. 388).

A dorsal muscle group is innervated by motor fibers of the second trigeminal (V_2 of Luther, 1909 and Holmgren, 1942; *T. maxillaris* of Jarvik, 1980, vol. 2), whereas the remaining muscles are innervated by the third trigeminal branch (*r. mandibularis* V_2 or V_3). The presence of motor fibers in the chimaeroid second trigeminal is unique among gnathostomes, but they occur in the equivalent (subocular) nerve ramus of *Petromyzon* (Holmgren, 1942, p. 250). In modern sharks the labial musculature is innervated only by the third trigeminal branch (Luther, 1908).

Although it is not possible to arrive at any definite conclusions regarding labial musculature and innervation in *H. basanus,* there are striking similarities between the arrangement and number of labial elements in this form and modern chimaeras, if the "prelabial," "premaxillary," and "premandibular" cartilages of the last are included. The general arrangement of labial cartilages in *H. basanus* may be more generalized than in chimaeras inasmuch as many of the labial elements are oriented more or less parallel to the jaw rami and gill arches.

Theories of homology between certain labial cartilages of chimaeras and sharks have been proposed from time to time, although

the embryological data are inadequate. There are consequently almost as many theories as authors on the subject (fig. 17). In the absence of reliable embryological data there is little hope of testing the plausibility of these theories. Nevertheless any theory concerning homology between shark and chimaeroid labial cartilages should not be refuted by *H. basanus*. Topographically the two upper labial cartilages of *H. basanus* resemble those of modern sharks in that one element is external to the other. The outer labial of *H. basanus* may thus be homologous with the anterior upper labial of modern sharks. The element internal and anterior to it in *H. basanus* may be either the equivalent of the posterior upper labial of modern sharks (particularly that of the embryo; fig. 17I), or else another element not represented in extant forms (fig. 17H). In the latter case, the small "articular" labial of *H. basanus* may represent the posterior upper labial of modern sharks. This interpretation is consistent with Hubrecht's (1876) and Allis's (1917) theories of homology between shark and chimaeroid labial cartilages (fig. 17A, D, H). The anterior upper labial of modern sharks would be homologous with the external upper labial of *H. basanus* and with the "e" cartilage (*sensu* Hubrecht; = "pre-maxillary cartilage" of Holmgren, 1942) of *Chimaera*. The internal upper labial of *H. basanus* would be represented in *Chimaera* by Hubrecht's cartilage "f/g" ("prelabial cartilage" of Holmgren) and would have no equivalent in modern sharks unless it has become incorporated into the nasal complex (cf. fig. 17A, D, G, H).

All these previous theories of homology inherently require the chimaeroid upper labials ("e" and "d") to transpose their positions ontogenetically, as in modern sharks. From available evidence it is simply not possible to determine whether this is actually the case, however. If future embryological studies reveal that this transposition does not occur, it is difficult to see how cartilage "d" (="superior maxillary") of *Chimaera* can be homologous (either in whole, or in part, or in conjunction with other cartilages) with the posterior upper labial of modern sharks. These theories would not be refuted, however, if transposition of elements "e" and "d" occurs in chimaeras. In this event, the upper labials of *Hybodus basanus* would differ from those of modern sharks and chimaeras, because (a) if its upper labials have not undergone transposition the internal "anterior" upper labial of *H. basanus* is homologous with the posterior upper labial of modern sharks and with the superior maxillary cartilage of chimaeras, or (b) if transposition did occur in *H. basanus*, its internal upper labial is not represented among the labials of modern sharks, as already discussed. Previous theories of homology between shark and chimaeroid labials are clearly inadequate, and data from *H. basanus* show that the labial cartilages of sharks can approach those of chimaeras in complexity.

The question of whether labial cartilages represent segmental premandibular visceral arches involves detailed embryological studies and comparison of various organ systems (e.g., nervous, vascular, musculoskeletal) that are beyond the scope of this work. The idea that premandibular arches were primitively present in chordates stems from Gegenbaur's (1872) hypothesis that shark labial cartilages represent parts of two premandibular arches. This view was opposed by Balfour (1885) who, while accepting that labial cartilages are premandibular in position, denied the existence of true pre-oral arches and proposed that the present gnathostome mouth is the primitive oral opening. According to Balfour (1885, p. 597), labial cartilages represent vestiges of a primitive suctorial mouth skeleton which originally occupied a pre-oral position, like the pre-oral suctorial apparatus of *Lepisosteus* larvae.

Gegenbaur's (1872) hypothesis is supported by the contention that labials correspond to extrabranchial cartilage (e.g., gill rays) of the postmandibular visceral arches (Parker, 1879; Bjerring, 1977; Jarvik, 1980). Such premandibular arches, however, would be unusual in being associated with stomodeal ectoderm rather than pharyngeal endoderm like the hyoid and gill arches (Goodrich, 1930). At present all that can be said is that in sharks the labial blastemas seem to be of epidermal, not visceral arch origin (Jollie, 1971); and that innervation of the dorsal group of labial muscles in chimaeras is consistent with the view that the labial cartilages are premandibular, but again not necessarily

of visceral arch origin (although the maxillary branch of the trigeminal nerve resembles the post-trematic innervation of a visceral arch inasmuch as both sensory and motor fibers are present).

Palatoquadrates

In *H. basanus* the palatoquadrate is not in contact with its antimere symphyseally (figs. 4B, 6B, 16). In little disturbed specimens the internasal keel partly separates the palatoquadrates anteriorly. Immediately behind this region, the dorsal margin of the palatoquadrate rises steeply beneath the ethmopalatine process of the neurocranium, and is flattened into a broad platform which probably represents a load-bearing surface at the front of the jaw. Some support would also have been given by the sides of the internasal keel. Thus there is a well-developed palatoquadrate articulation with the preorbital region of the braincase (see above; cf. Woodward, 1889a, 1916).

Behind the ethmoid region the palatoquadrate expands dorsally into the floor of the orbit, above the suborbital shelves. It slopes laterally so that its lower (tooth-bearing) margin, with its dental groove (figs. 4B, 7A) lies much farther laterally than the dorsal margin, which is tucked up against the interorbital wall. Although the palatoquadrate deepens within the orbit, there is no orbital process in *H. basanus.* There is a rounded process on the anterior dorsal margin of the palatoquadrate of *H. hauffianus* but it seems to represent part of the ethmoidal articulation rather than a more posterior orbital one (Maisey, 1982). This is important since DeBeer (1931, p. 628; 1937, p. 419) regarded the orbital process of *Chlamydoselachus* as part of a second articulation, posterior to the ethmoidal articulation. An orbital articulation of the type found in orbitostylic sharks (*Chlamydoselachus,* hexanchoids, squaloids, *Pristiophorus,* and *Squatina*) is apparently absent in hybodonts (Maisey, 1980). The dorsal process of *H. hauffianus* should not be called an orbital process; nor, in my view, should the small process on the anterior end of the palatoquadrate in *Xenacanthus* or "*Cladodus.*" It clearly has no relationship to any articular surface on the interorbital wall, but is part of the more anterior ethmoidal articulation (cf. Jarvik, 1977, 1980). This is also true of the "orbital process" in *Tristychius*; Dick (1978, p. 84) comments that "the orbital process lies slightly anterior to the orbit." The optic foramen is situated much farther posteriorly. In orbitostylic living sharks the orbital process of the palatoquadrate articulates with the interorbital wall just behind the optic nerve and anterior to the optic pedicle, rectus muscle complex, and (more significantly with regard to fossils) the foramen for the efferent pseudobranchial artery (Maisey, 1980). No articular surfaces are present in this vicinity in *H. basanus, Xenacanthus, Tamiobatis,* "*Cladodus,*" *Tristychius,* or *Cobelodus* or among living galeomorphs or batoids.

The posterior part of the palatoquadrate of *H. basanus* is contoured to fit closely against the floor of the braincase, but a postorbital articulation (as occurs in hexanchoids and many Paleozoic selachians) is absent. There is a lateral quadrate expansion, the dorsal surface of which underlies the postorbital process, while its ventral surface roofs over a deep adductor fossa. In lateral view the palatoquadrate is constricted dorsoventrally toward the front of the adductor fossa (figs. 2C, 16C). Posteriorly there is a flattened surface over which the hyomandibula sits (figs. 4A, C, 5, 6C, 16C, E). A large articular process (Hotton, 1952) at the extreme posterolateral extremity of the quadrate flange articulates with a cotylus in the lower jaw. Mesial to this the palatoquadrate has a weak quadrate concavity for an articular knob on the lower jaw. Thus there is a "double" selachian-type articulation *sensu* Gegenbaur (1872) but the lateral component is less developed in *H. basanus* than in xenacanths and Recent sharks (see Allis, 1923; Hotton, 1952). This is also true of the Liassic hybodont BM(NH) P50869 and *Asteracanthus* sp. palatoquadrates, BM(NH) 12614. There is general agreement in the shape of the palatoquadrates between *H. basanus, H. hauffianus, H. delabechei, H. fraasi,* and *Acrodus* sp., although in most cases these elements are preserved flat (Maisey, 1982). In *Hybodus* and *Acrodus* sp. (and probably *Palaeobates,* according to Stensiö's 1921 figure of the lower jaw) the teeth lie in a dental groove, as in *Heptranchias.* In *Asteracanthus* [e.g., BM(NH) 12614;

see also Peyer, 1946], there is no dental groove, much of the molariform dentition instead being borne on the large expansions from the jaw cartilages, particularly in the case of the palatoquadrates (Maisey, 1982, fig. 8).

Thus the palatoquadrate of *H. basanus* agrees in many respects with that of other Mesozoic hybodonts in having a strongly buttressed ethmoidal articulation, deep adductor fossa and low otic region, and palatoquadrate morphology is evidently different from that of other sharks (Maisey, 1980, 1982). There is no evidence of a postorbital articulation in *H. basanus,* but Thomson (personal commun.) finds a transverse groove on the low otic region of a Triassic hybodont palatoquadrate from Madagascar. Interestingly, Dick (1978) found a similarly positioned ridge on the palatoquadrate of *Tristychius,* which he interpreted as a postorbital articulation, located on the ventral surface of the postorbital process. Comparison of the palatoquadrates of *H. basanus* and Thomson's hybodont suggests that the latter had a postorbital articulation beneath the postorbital process, as in *Tristychius.* In other sharks where a postorbital articulation is present, it is situated on the posterior wall of the postorbital process. The unusual location of this articulation in *Tristychius* may therefore be a character uniting it with primitive hybodonts (corroborating other characters used by Dick, 1978, such as the presence of calcified ribs and certain features of the finspines; but see Maisey, 1982, for an alternative view).

Meckel's Cartilage

Woodward (1916) had very few comments on the Meckel's cartilage of *H. basanus*: "The rami of the mandible, though deep and massive behind, rapidly taper forwards and meet at their comparatively feeble symphysis, which does not extend so far as the end of the upper jaw."

The lower jaw is slightly shorter than the upper. When the mouth was tightly closed, the lower jaw fitted just inside the upper, and the teeth interlocked as in modern predaceous sharks (figs. 2C, 6A, B, 7C). The symphysis is certainly weak, although it is extensive (figs. 2B, 6E, 7B). Lateral to the symphysis is a vague, shallow groove running posteriorly from near the front of the lower jaw. This is occupied by an elongate lower labial cartilage. The groove dies away about halfway along the jaw, and is delimited dorsally by an outward bulge which reflects the position of the dental groove mesially on the cartilage. In lateral view the lower jaw rises posteriorly into a low eminence forming the posterior margin of a posterolateral articular cotylus into which the articular process of the palatoquadrate fits. Anterior to this is a pronounced mandibular knob, fitting into the quadrate cavity. On its visceral surface, Meckel's cartilage has a pronounced ridge passing ventrally from the mandibular knob (figs. 5, 16E). The ridge, termed here the internal mandibular ridge, is characteristically present in sharks. It loosely defines the anterior limit of a shallow, concave area (termed here the internal mandibular concavity) on the visceral surface of the mandible, ventral to the articular cotylus. In modern sharks the internal mandibular concavity is occupied by the proximal end of the ceratohyal and by the mandibular ligament. This ligament passes viscerally over the internal mandibular ridge, and attaches to the palatoquadrate (Häller, 1926). Relative development of the secondary joint (mandibular knob and quadrate concavity) and of the internal mandibular ridge and concavity is highly variable among Recent and fossil sharks (Maisey, in preparation). *Adductor mandibulae* muscles would have been attached to the lateral surface of Meckel's cartilage as in other sharks, an arrangement which is probably primitive for gnathostomes (Lauder, 1980).

Hyoid Arch

Where a postorbital articulation is well developed, as in *Heptranchias, Xenacanthus,* and *Acanthodes,* the hyomandibula is directed posteriorly and to some extent ventrolaterally, more or less parallel to the dorsal margin of the palatoquadrate otic process. The hyomandibula retains this orientation in elasmobranchs such as *Chlamydoselachus,* even though a postorbital articulation is absent. The hyomandibula is largely obscured by the palatoquadrate in lateral view. In many other modern elasmobranchs (especially in

forms where the jaws are relatively short and oriented in a transverse plane), the hyomandibula is more visible in lateral view. The hyomandibula is also exposed in this way in *Tristychius* (Dick, 1978) and *H. basanus* (Woodward, 1916). In *H. basanus,* however, the arrangement of the hyoid arch and its relationship to the jaws and braincase have not until now been critically examined, although a brief account of the role of the hyoid arch in the jaw suspension of *H. basanus* has appeared elsewhere (Maisey, 1980). In *H. basanus* the hyomandibular articulation is fully exposed on the side of the head, while the otic region of the palatoquadrate is partially concealed by the postorbital process (figs. 6C, D, 16 C, E). Several articulated specimens show the position of the hyomandibula, e.g., BM(NH) P60110, BM(NH) P13094. Despite this, Woodward's (1916) restoration attempted to tuck the hyomandibula behind the palatoquadrate, as did my own restoration before the cranium and jaws of BM(NH) 40718 were separated. In this specimen the palatoquadrate otic process almost meets the braincase behind the postorbital process, and there is no room for a hyomandibula between them.

The hyomandibula is clublike in lateral view, with a broad, anteriorly directed proximal end (figs. 4D, 6C, D). As Woodward (1916, pp. 6–7) noted, it is a slender cartilage, slightly compressed laterally. Its characteristic shape readily distinguishes it from other visceral arch elements. The proximal articular surface is rounded, fitting into a depression on the side of the otic capsule. Both hyomandibulae of BM(NH) P11870 (Woodward, 1916, pl. 11, figs. 1 and 1A; and fig. 6C–E here) are *in situ.* The head of the left hyomandibula is preserved almost *in situ* in BM(NH) 40718. The hyomandibula meets the ceratohyal just behind the jaw-joint, in the usual selachian configuration. Only dorsally does the hyomandibula overlie the palatoquadrate. Seen from behind this arrangement is less peculiar than the lateral view suggests (fig. 16E). The ceratohyal extends from behind the jaw-joint to just behind the Meckelian symphysis. A basihyal separates the ceratohyals (Woodward, 1889a, pl. 12, fig. 3; see fig. 2B here). Anteriorly the ceratohyals have expanded articular surfaces (figs. 2B, 16) and resemble the ceratobranchials except that the latter are concavo-convex in cross-section with the mesial surface concave. Hyoidean gill-rays are well developed in the Liassic hybodontid BM(NH) P50869; at least six are still attached to the right ceratohyal. These rays are not known in *H. basanus.*

In living elasmobranchs the hyoid and mandibular arches are always united ligamentously in the vicinity of the jaw-joint. More specifically, the ceratohyal of the hyoid arch is strongly tied, by means of ligaments, to Meckel's cartilage (Gadow, 1888; Allis, 1923). In some living elasmobranchs the hyomandibula articulates with the mandibular knob of Meckel's cartilage (e.g., *Squalus*); this is generally considered to be a derived condition. Hotton (1952) has summarized the variability of this union between the hyoid and mandibular arches in elasmobranchs as follows:

"in living forms with well developed quadrate concavities there is no direct ligamentous connection between the mandibular knob and the hyomandibular cartilage, although in *Heterodontus* a process of the latter abuts against the mandibular knob. In more advanced forms, in which the quadrate concavity is poorly developed or lacking, a strong ligament connects the mandibular knob with the hyomandibular cartilage."

Hotton (1952) also proposed that the hyomandibula of modern hexanchoids is not suspensory, because it lacks an articulation and/or a ligamentous attachment with Meckel's cartilage. Nonetheless, the hyomandibula and ceratohyal of all living elasmobranchs are united by an articulation and by ligaments, and the hyoid arch as a whole therefore contributes to jaw support. This support ranges from the almost exclusively hyoidean suspension of batoids at one extreme, to the far simpler condition where the hyoid arch offers some lateral limitation to jaw eversion, but little else (e.g., *Notorhynchus*; Katherine Wolfram, personal commun., and in preparation). Thus even where a hyomandibula is "non-suspensory" (*sensu* Hotton, 1952), the hyoid arch contributes to jaw support, and is therefore functionally hyostylic (Maisey, 1980).

Hotton (1952) interpreted the hyomandibula of *Xenacanthus* as lacking an articulation and presumably any ligamentous attachment

with the mandibular knob of Meckel's cartilage. Unfortunately, Hotton's study was based on disassociated remains, but a complete head, with jaws and hyoid arch intact (MCZ 12872, figured in Schaeffer, 1981, fig. 1) seems to corroborate Hotton's view. Articulated *H. basanus* heads [particularly BM(NH) P60110] suggest that, as in *Xenacanthus,* the hyomandibula did not articulate with the mandibular knob of Meckel's cartilage. In both *H. basanus* and *Xenacanthus* the mandibular knob is situated away from the distal end of the hyomandibula, whereas the auxiliary jaw articulation is markedly anterior to the primary lateral one. Jaw suspension in *H. basanus* resembles that of most living elasmobranchs in that the postorbital articulation is lost, the palatoquadrate lacks a big otic process, and the hyomandibula serves as the only direct endoskeletal link between the neurocranium and mandibular joint; but unlike the majority of these modern elasmobranchs, *H. basanus* has not acquired a strong articulation between the hyomandibula and the mandibular knob of Meckel's cartilage. As hexanchoids illustrate, however, such an articulation is not a corollary of jaw support by the hyoid arch.

It is difficult to make comparisons between *H. basanus* and other fossil sharks. In *Tristychius* the mandibular knob ("mandibular process" of Dick, 1978) seems to have lain only slightly anterior to the primary articulation, but it is doubtful whether the hyomandibula and mandibular knob actually met.

According to Zangerl and Williams (1975) the hyomandibula of *Cobelodus* did not meet the jaw-joint distally, and this form has consequently been considered aphetohyoidean (*sensu* Watson, 1937). Their argument rests on the way in which the visceral arches are reconstructed. Even without an involved discussion of alternative arrangements, however, it is clear from the preceding comments that lack of a hyomandibular articulation with Meckel's cartilage is not an indicator of aphetohyoidy. *Notorhynchus* is not aphetohyoidean, nor are chimaeras, and presumably nor were *Xenacanthus* or *Hybodus.* There is no evidence that the ceratohyal of *Cobelodus* lacked ligamentous connections with Meckel's cartilage, and the hyomandibula articulated with the neurocranium as in other sharks. It is therefore concluded that the hyoid arch of *Cobelodus* offered just as much jaw "support" as in hexanchoids, even if the distal end of the hyomandibula lay some distance behind the jaw joint in *Cobelodus.* There is every indication in the Tennessee cladoselachian (NMNH 20675) that the hyomandibula terminated distally much closer to the jaw-joint than Zangerl and Williams (1975) indicate in *Cobelodus,* but it is not yet established whether the mandibular knob made contact with the hyomandibula in the cladoselachian.

Cleaning the hyoid arch elements of BM(NH) P60110 has provided further data on the ceratohyal and "basihyal" of *H. basanus.* The end of the ceratohyal adjacent to the jaw-joint is hollowed out on its lateral surface, forming a deep pocket. The function of this pocket is unknown although it probably provided an attachment for ligaments uniting the hyoid and mandibular arches. It is unlikely to have housed the equivalent of an *adductor branchialis* muscle since no modern shark, ray, or chimaeroid possesses an *adductor hyomandibularis* muscle (Edgeworth, 1935). A similar but shallower pocket is noted on some galeomorph ceratohyals, and there seems to have been a deep pocket in *Xenacanthus* ceratohyals from Texas.

The "basihyal" of *Hybodus basanus* is a large, rounded element with a flat upper surface which was covered in denticles (AMNH 4692). Ventrally the "basihyal" is hollowed out by a pair of extremely large concavities separated only by a thin vertical septum of calcified cartilage. This septum broadens anteriorly to form a wide anterior margin which slopes steeply away from the flat upper surface. Posteriorly the septum again broadens, but not nearly so much as anteriorly. The ceratohyals articulate with the ventrolateral sides of the "basihyal," on either side of the paired concavities. The first ceratobranchial articulates with the posterior margin of the "basihyal." A more complete description of the visceral skeleton of *H. basanus* is planned, after preparation of additional material.

Jaw Suspension and Feeding Mechanism

The jaw suspension of *H. basanus* not only differs from those patterns found in modern elasmobranchs, but also from the suspenso-

rial arrangements found in many other fossil sharks, such as *Xenacanthus, Cladoselache,* and *Cobelodus.* Nonetheless, all these suspension patterns have several features in common. In particular, the ethmoid articulation is well developed, and posteriorly the mandibular and hyoid arches are intimately associated, so that support was probably given by the hyomandibula (either by direct articulation with Meckel's cartilage, or by means of ligamentous attachments).

Although the dorsal margin of the palatoquadrate in *Hybodus basanus* is contoured to fit closely against the braincase between the ethmoid and otic regions there is no evidence of any articular surfaces (e.g., orbital process, basitrabecular articulation). In *H. basanus*, the jaws seem to have been supported only by the ethmoid articulation and hyoid arch. Within the constraints of such a system, the possible jaw movements of *H. basanus* are briefly considered.

Anteriorly the dorsal ramus of the palatoquadrate is contained by the deep groove which is floored by the anterior part of the palatobasal ridge and roofed by the ethmopalatine process. There is no indication of ridges and grooves on either the palatoquadrate or the braincase in this region (cf. *Cobelodus, Xenacanthus,* and various other Paleozoic sharks; see Zangerl and Case, 1976; Schaeffer, 1981). Thus the palatoquadrate of *H. basanus* was probably free to slide anteroposteriorly and also laterally with respect to the ethmoid groove. Examination of the ethmoid region in *H. basanus* gives no indication as to the limits of such movements, however. Probably the greatest constraints were made by the hyomandibula because of its position behind the large, downturned postorbital process. This position imposes restrictions upon anteroposterior movement. Nevertheless, the hyomandibular articulation with the braincase would permit lateral movement, allowing the mandibular joint to swing outward. According to Moss (1977, p. 358), this type of lateral hyomandibular movement is present among those modern sharks where the hyomandibula is elongated and directed posteriorly from the braincase. Such movement serves to increase the gape laterally and also to maximize its vertical extent. In lamniforms and carcharhiniforms the movement also introduces an anterior rotation to the biting mechanism. Such movement is apparently not possible in orbitostylic (*sensu* Maisey, 1980) sharks, where the palatoquadrate orbital process articulates with the interorbital septum. Even in hexanchoids, where the hyomandibula is long and posteriorly directed, palatoquadrate movement is confined to a vertical plane with respect to the neurocranium (Moss, 1977). As previously discussed, an orbital process of this type is absent in *H. basanus.* It is concluded that, despite several differences in the configuration of the jaws and braincase between carcharhiniforms and lamniforms on one hand, and *H. basanus* on the other (notably the much stronger ethmoidal support of the latter), jaw movement in *H. basanus* probably resembled that occurring in these modern sharks more than in any other.

Modern studies of feeding mechanism in sharks support Balfour's (1885) view that labial cartilages are an important part of a suctorial mechanism (Tanaka, 1973; Compagno, 1973; Moss, 1977). In *Ginglymostoma* the lower and posterior upper labial cartilages are united by a fairly strong muscle, which acts to extend the sides of the mouth into a tubular shape (Moss, 1977, p. 361). The *M. coracobranchialis* and *M. coracohyoideus* are prominent and serve to enlarge the pharynx during prey ingestion, whereas the *M. coracomandibularis* is comparatively small. As discussed earlier, the prominent labial cartilages of *H. basanus* suggest that labial musculature was also well developed in the side of the mouth. Therefore, it is quite likely that *H. basanus* was in part a suctorial feeder, like *Ginglymostoma.* This is a curious combination of features since *H. basanus* seems to have been capable of limited lateral jaw movement combined with some rotation, like modern lamniforms and carcharhiniforms, as well as possessing a suctorial mechanism of the type found in orectoloboids. While Moss (1977) considered the "suction-crushing" suctorial feeding mechanism of orectoloboids to be distinct from the "gouging" rotational mechanism of lamniforms and carcharhiniforms, it is significant that he regarded the former mechanism as a modification of the latter (Moss, 1977, fig. 5). In many sharks, including hexanchoids and squaloids, the *M. coracohyoideus* is more prominent than the *M. coracomandibularis,*

suggesting that dilation of the pharynx is more than simply an aid to allowing the mouth to open. Moss (1977, p. 360) speculated that suction may play an important part in squaloid feeding mechanisms. In fact, it is possible that a suctorial mechanism is primitively present in elasmobranchs, as Balfour (1885) implied, but has become reduced in various raptorial feeders. Such a mechanism would be particularly useful among early sharks, whose jaw suspension is generally visualized as being fairly rigid (Gross, 1937, 1938; Harris, 1938; Hotton, 1952; Schaeffer, 1967, 1981; Zangerl and Williams, 1975). *Hybodus basanus* lacks a postorbital palatoquadrate articulation; apparently it has achieved this condition independently of modern hyostylic sharks (Maisey, 1980, 1982), and any rotational jaw movement would consequently also seem to have been secondarily acquired, while its primitive suctorial mouthparts have become elaborated. Thus *H. basanus* was probably in part a suctorial feeder, at least during the earliest phases of ingestion, but was probably able to seize quite large prey. The only direct evidence of hybodont prey is seen in *H. hauffianus,* which consumed quantities of belemnites (Brown, 1900, pl. 16, fig. 1). The jaws of this species seem to resemble those of *H. basanus* closely (Maisey, 1982). It must be remembered, however, that the jaws and dentition of different hybodont genera display considerable variation, so that the preceding comments on the jaw suspension and feeding mechanism in *H. basanus* may be inapplicable to other hybodonts such as *Asteracanthus,* a form which has a molariform dentition and peculiarly modified palatoquadrates (Peyer, 1946; Maisey, 1982).

Branchial Skeleton

Hybodus basanus has five gill arches behind the hyoid arch, in common with many living sharks (Woodward, 1889a, p. 274; 1916, p. 8). In BM(NH) P2082 and BM(NH) P11872 the ceratobranchials are visible; epibranchials are also exposed in BM(NH) P2082. There is no sign of calcified basibranchials, hypobranchials, pharyngobranchials, or extrabranchials.

The ceratobranchials and ceratohyals are similar, and form a continuous series gradually diminishing in diameter and length posteriorly. Their diameters in BM(NH) P2082 are as follows: Ceratobranchial I—15 mm.; II—10 mm.; III—8 mm.; IV—5 mm.; V—2 mm.

Each ceratobranchial is separated from its antimere by a broad space, and presumably were separated by uncalcified hypobranchials and basibranchials. The gill arches have invariably collapsed dorsally into the oralobranchial chamber, but remain in sequence. Although pharyngobranchials are unknown in *Hybodus basanus* they are present in *H. hauffianus* (Koken, 1907) and *H. cassangensis* (Maisey, 1982). There is no evidence of calcified gill rays in *H. basanus.*

The only other fossil sharks in which pharyngobranchials have been described in some detail are Permian xenacanths from Germany (Koken, 1889; Fritsch, 1889, 1895; Jaekel, 1895, 1906). These are also the only fossil sharks in which the hypo- and basibranchial skeleton is reasonably well known. Although there are discrepancies between various accounts, all but Jaekel (1906) agree that the hypobranchials are posteriorly directed as in modern elasmobranchs. Jaekel (1906, figs. 1, 2) shows these elements directed forward, as in osteichthyans and acanthodians (see Miles, 1968; Nelson, 1968, 1969; Moy-Thomas and Miles, 1971). Jaekel (1895) figured paired hypohyals in an unspecified (hypothetical?) xenacanth. Such structures have not been reported in modern elasmobranchs, *Cobelodus, Cladoselache, Hybodus hauffianus,* or xenacanths described by Fritsch (1895), and they have not been found in *H. basanus.*

Inside the crushed oropharyngeal region of one *Hybodus basanus* specimen, BM(NH) P6356, are fragments of calcified gill filaments. Preservation of these structures has not previously been reported in fossil sharks. The morphology of these filaments is not clear, as few pieces remain intact, but they do not seem to have been as slender and elongated, or as numerous as in *Chlamydoselachus* (Allis, 1923) or *Notorhynchus* (Daniel, 1934). Gill filaments are also preserved in the Tennessee cladoselachian, NMNH 20675, and are clearly short, as in *H. basanus* and *Squatina,* despite the presence of extremely long supporting gill rays. The apparent similarity in size, shape, and low number of gill

filaments between *H. basanus* and cladoselachian specimens contradicts the view that the greater number of gill filaments in *Notorhynchus* is a generalized condition (Daniel, 1934, p. 149). It is not possible to determine whether in *H. basanus* the filaments of the posterior demibranch are longer than those of the anterior, as is generally the case in modern elasmobranchs.

ENDOSKELETAL CALCIFICATION IN *HYBODUS BASANUS*

The cranial endoskeleton of *H. basanus* is perichondrally calcified by a layer of prismatic apatite calcifications as in modern elasmobranchs, where this layer forms a loosely attached sheath to the unmineralized cartilage (Moss, 1977). This prismatic layer is easily damaged (or even entirely removed) when a shark skeleton is prepared by maceration, yet it is all that remains of the endoskeleton in fossil sharks. In most modern chondrichthyans there is only a single layer of these prisms, although complex invaginations of the perichondrium may result in apparently doubling-up of layers (e.g., in the pristid rostrum; Casier, 1949). Experimental work has shown that there is a high turnover rate of apatite in the prismatic tissue, suggesting a constant remodeling process (Applegate, 1967), although the details of this process are not understood. Individual prisms are united by radiating bundles of collagen fibers (Bargmann, 1939; Kemp and Westrin, 1979), and it seems likely that the skeletal enlargement is in part accomplished by growth of individual prisms (Schaeffer, 1981).

In many Paleozoic sharks more than one layer of perichondral prisms is usually present. This condition has been found in Permian xenacanths (Fritsch, 1889, p. 191, figs. 176–180; pl. 90, fig. 6B; Schaeffer, 1981, p. 33, fig. 17), *Ctenacanthus compressus* (AMNH 189), *Tamiobatis* sp. (AMNH 2140; Schaeffer, 1981, fig. 22); in various indeterminate shark jaws and visceral arch components from the St. Louis Limestone of Illinois (AMNH 106 and 107; NMNH 299647), in stethacanthids from the Pennsylvanian of Arkansas (Maisey, in preparation), and in an indeterminate elasmobranch from the late Cretaceous of Kansas (UNMNH 1P 16868). Furthermore, there are reports of multiple layering in *Orodus* sp. (Rainer Zangerl, personal commun.). In *Hybodus basanus* there is generally only a single layer of perichondral prisms over the neurocranium, jaws, and visceral arches, but there is evidence of two or three prism layers around the posterior semicircular canals and in the basicranium of AMNH 4692. The occipital region in a specimen of *Hybodus reticulatus,* BM(NH) P2203d, is also strongly calcified and apparently has several layers of perichondral prisms. This disjunct occurrence of multiple prism layers in various sharks makes it impossible to use multiple layering *per se* as a synapomorphy of xenacanths and ctenacanths (cf. Schaeffer, 1981, p. 62). Nevertheless, only in xenacanths, *Tamiobatis* and ctenacanths is the neurocranium heavily mineralized by numerous prism layers; in other forms the jaws and visceral arches may be heavily calcified, but there are generally few prism layers in the neurocranium. The phylogenetic implications of this character distribution are obscure, however. Multiple prism layering does not seem to be a simple growth-related phenomenon.

THE DERMAL SKELETON

Teeth

Preparation of BM(NH) P6356 and AMNH 4692 verifies the dental variation already noted by Woodward (1916) and Patterson (1966). All teeth are multicuspid and sharply pointed, even those from the posteriormost files (figs. 7, 18). The central cusp inclines progressively farther posteriorly in tooth files nearer the jaw-joint. As many as three or four pairs of lateral cusps are usually present, although there may be fewer (see below), and all but the outermost pair are strongly striated. Striations extend almost to the tip of the central cusp lingually, but are often less extensive labially.

The basal plate of each tooth is penetrated by numerous unevenly distributed foramina. The lingual margin of the basal plate extends as a small lingual torus, somewhat as in *Synechodus, Palaeospinax,* and cladodont teeth but never to the same extent. No specialized foramina are present in the basal plate of *H. basanus* teeth (Patterson, 1966)

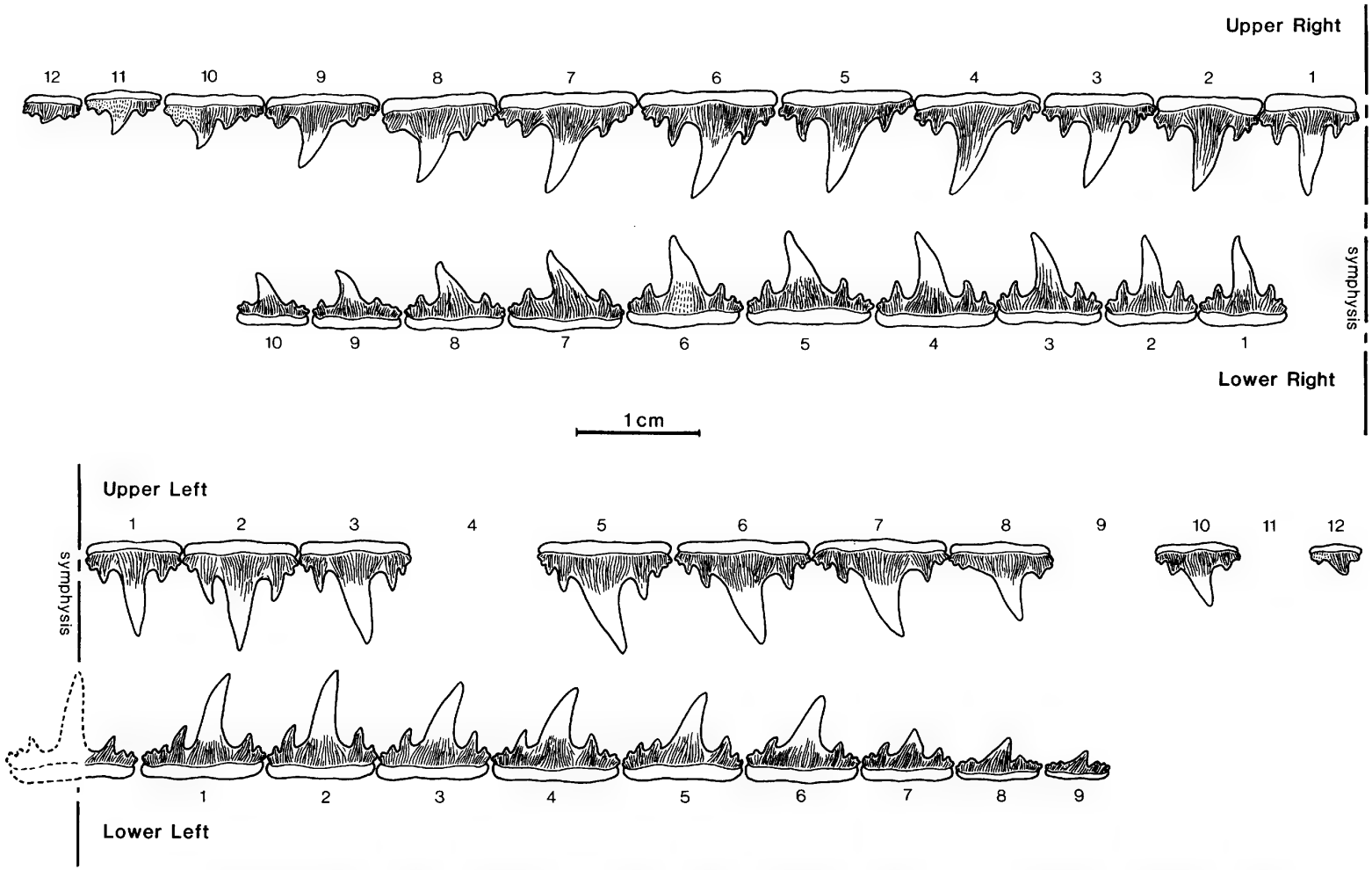


FIG. 18. *Hybodus basanus* dental variation, from AMNH 4692. The first or second functional tooth is illustrated from each replacement series. All teeth are drawn to scale; note size discrepancy between left and right teeth. For other variation see text and figure 20.

Neither Woodward (1916, 1919) nor Patterson (1966) has figured a complete dentition of *H. basanus*. I have therefore included an outline restoration, based on AMNH 4692, to illustrate the general tooth form, the number of tooth files, absence of an upper symphyseal series, and alternation of upper and lower teeth (fig. 18). This represents the first detailed account of a complete hybodont dentition based on an individual specimen. Previous accounts of hybodont dentitions are either based on incomplete material (e.g., Woodward, 1889a; Peyer, 1946) or are restorations of disassociated teeth (e.g., Patterson, 1966).

Among living elasmobranch species there can be considerable variation in the dentition, e.g., in number of tooth rows (Gudger, 1933, 1937; Applegate, 1965; Sadowsky, 1970; Taniuchi, 1970; Reif, 1976), in the number of accessory cusps (Gudger, 1937; Sadowsky, 1970; Taniuchi, 1970), between sexes (Bigelow and Schroeder, 1953; McEachran, Boesch, and Musick, 1976; Thomson, Findley, and Kerstitch, 1979; McCourt and Kerstitch, 1980). Moreover, tooth replacement may be orderly and regulated, e.g., *Dalatias, Isistius,* or it may be localized, with adjacent tooth files operating at different replacement rates, e.g., many lamnoids (Landolt, 1947; James, 1953; Strasburg, 1963). In addition to all this "normal" variation, dental abnormalities have also been reported, mostly examples of tooth pattern reversal (Gudger, 1937; Compagno, 1967; Reif, 1978a, 1980). Therefore to study the dentition of an individual fossil shark might seem hopeless, in the face of so many formidable possibilities for variation. Taxonomic studies of fossil sharks are certainly unreliable when based solely upon teeth. For example, White's (1931) subdivision of odontaspids into subgenera *Odontaspis, Synodontaspis,* and *Parodontaspis* is founded upon characters that all fall within the observed variation of the living sandshark *Carcharias taurus* (Applegate, 1965; Sadowsky, 1970; Taniuchi, 1970). Similarly, variation within the dentition of *H. basanus* seems broad enough to include teeth which have previously been referred to distinct species, e.g., *H. ensis, H. parvidens* (Woodward, 1916; Patterson, 1966).

In order to make a meaningful study of *H. basanus* teeth, the dentition of AMNH 4692 is described, as it represents the best preserved example. Following this description some comments on variation between this and other individuals are made, since it is often possible to compare parts of several dentitions even though the entire array is not visible.

The dentition of AMNH 4692 is shown in figures 7A, B, and 18. Additional teeth from other individuals can be seen in figure 7C and D. In AMNH 4692 10 replacement series of teeth have been identified in the upper right dentition, and 11 or 12 in the upper left. In all probability there were 11 or 12 series in the upper right ramus, but small posterior teeth like those in the upper left dentition have not been discovered. Ten series are present in each lower ramus, but the first series in the lower left dentition is broken and may correspond to the symphyseal series of other specimens. In AMNH 4692, however, this series does not align with the symphysis [symphyseal teeth of BM(NH) 6356 are shown in fig. 7C].

Teeth of adjacent series are arranged alternately, as in many carcharhinoids. Thus teeth in any given replacement series cannot

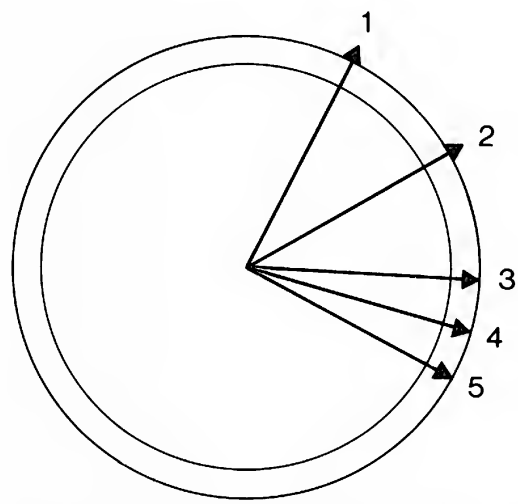


FIG. 19. Rotation diagram for *Hybodus basanus* lower right anterior teeth, from measurements of AMNH 4692. Convention of diagram after James (1953). Teeth 1 and 2 are considered functional; remaining teeth lie within dental groove and are non-functional.

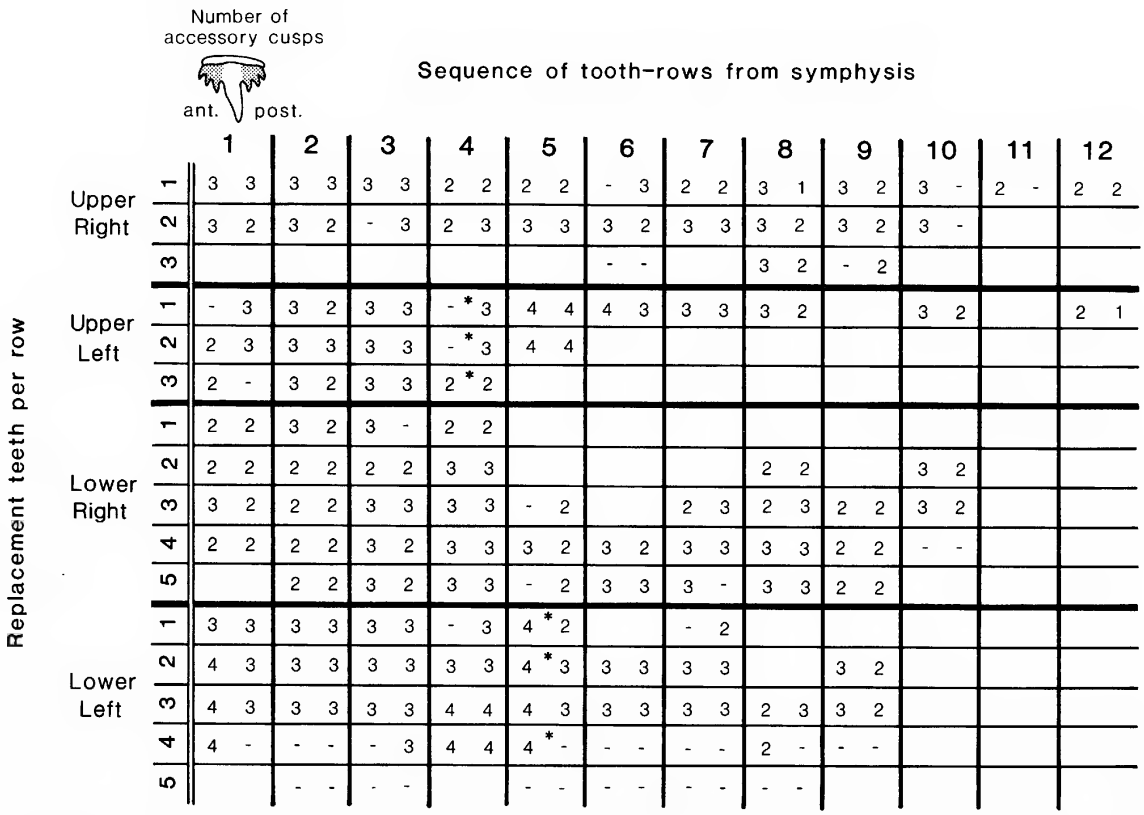


FIG. 20. Variation in lateral cusp numbers in all teeth of AMNH 4692. The dentition is considered as four quadrants (upper right, upper left; lower right, lower left) and replacement series are assigned numbers from front (1) to back (12). Successional teeth are sequenced labio-lingually (1–3 or 1–5), and the number of anterior and posterior lateral cusps are given for each tooth; thus each small rectangle represents a tooth. Short dashes indicate broken teeth (exact count unavailable); blank spaces indicate missing tooth. * indicates malformed tooth.

be lost until the preceding tooth in each adjacent file is shed (Strasburg, 1963, fig. 5B, D). The proximity of adjacent tooth series in *H. basanus* suggests that its dental lamina was continuous around the jaw arcade. Upper and lower tooth series are offset, so the teeth interlock when the mouth is closed (fig. 7C). There is no upper symphyseal series.

Within each replacement series there are two or three non-functional teeth and one or two in the functional position (fig. 7A, B). In AMNH 4692 the lingualmost teeth lack any basal platform, and sometimes the accessory cusps are found separately. These teeth evidently lay deepest within the dental lamina and represent the newest teeth, which were undergoing development at the time the shark died. It is possible to measure the rotational angles of the teeth in *H. basanus* (fig. 19) for comparison with living sharks (e.g., James, 1953). Teeth are rotated approximately 65° before they occupy an apparently functional position in *H. basanus,* and evidently remained attached to the jaw beyond 90° rotation. Few teeth are preserved with an apparent rotation of more than 90° (although in such an exposed position their chances of preservation *in situ* would be remote). This rotation corresponds closely with that documented in *Lamna* (James, 1953, fig. 8); there is no indication of an abrupt change in rotational angle from a non-functional to a functional position, as occurs in *Carcharhinus, Dalatias,* and modern hexanchoids.

It is difficult to distinguish anterior and lateral teeth, although the more posterior

lower laterals are decidedly stubbier and have steeply inclined cusps (fig. 18). The principal cusp of an anterior tooth has slightly stronger sinusoidal curvature in a labio-lingual direction than more lateral teeth. Accessory cusps are elongate and slender in the anteriormost five or six rows of upper and lower teeth, and reach a maximum length in the fifth; lateral teeth have lower, triangular accessory cusps. It is also difficult to distinguish upper and lower teeth. The principal cusp of an upper tooth is rounded in cross-section; in a lower tooth the cross-section is slightly broader and the principal cusp is therefore slightly more bladelike. The difference is not great, however, and would probably prove an unreliable means of distinguishing isolated teeth.

The tooth crown of *Hybodus basanus* is ornamented by many fine striae which often bifurcate basally. The lingual face of the crown is almost entirely striated, but according to Woodward (1916) and Patterson (1966) only the lower part of the principal cusp is striated labially. This is true only of the anterior teeth, however. Farther posteriorly the labial surface of the principal cusp is just as strongly striated as the lingual surface.

Figure 18 illustrates the variation in tooth shape and ornamentation in AMNH 4692. In most cases, either the first or second functional tooth in each series has been drawn. It will be noted that while principal cusp height becomes lower posteriorly, the vertical extent of striations on the labial surface does not diminish appreciably. The taller anterior teeth are therefore striated only proximally, whereas shorter posterior teeth are more completely striated. Large anterior teeth of *H. basanus* closely resemble teeth referred to *H. ensis* with respect to their striation patterns, whereas smaller posterior teeth of *H. basanus* agree with *H. parvidens* teeth in their ornament. Interestingly, *H. ensis* teeth are characteristically large, with a tall principal cusp, and teeth referred to *H. parvidens* are usually small, with a fairly low cusp (Woodward, 1916; Patterson, 1966). This raises the possibility that the supposedly specific differences between these teeth are merely reflections of different-sized individuals and of different topographic positions within the mouth.

Woodward (1916) and Patterson (1966) thought that the stratigraphic range of *Hybodus parvidens* was entirely below that of *H. basanus*. Remapping of the Bexhill area and the ostracod evidence (see "Materials and Methods") suggest that *H. basanus*-bearing deposits should be placed at lower stratigraphic levels (e.g., Wadhurst Clay or Ashdown Series; Professor P. Allen, personal commun.), as Charles Dawson suggested in his letter to Woodward. This would make *H. basanus* contemporaneous with *H. parvidens*. Patterson's (1966, p. 300) comment that *H. parvidens* "did not become extinct, but evolved into *H. basanus* by a further increase in crown height and in the number of striae, coupled with an increase in size" underlines the difficulty in separating these species; the same is true of the Wealden *H. ensis*, whose teeth "show a trend towards narrowing of the central cusp, sometimes accompanied by coarsening and lengthening of the striae which may produce teeth closely similar to those of

FIG. 21. *Hybodus basanus*, BM(NH) P6356, dorsal view of endolymphatic fossa, showing scales and muscle fibers. Anterior toward top of figure.

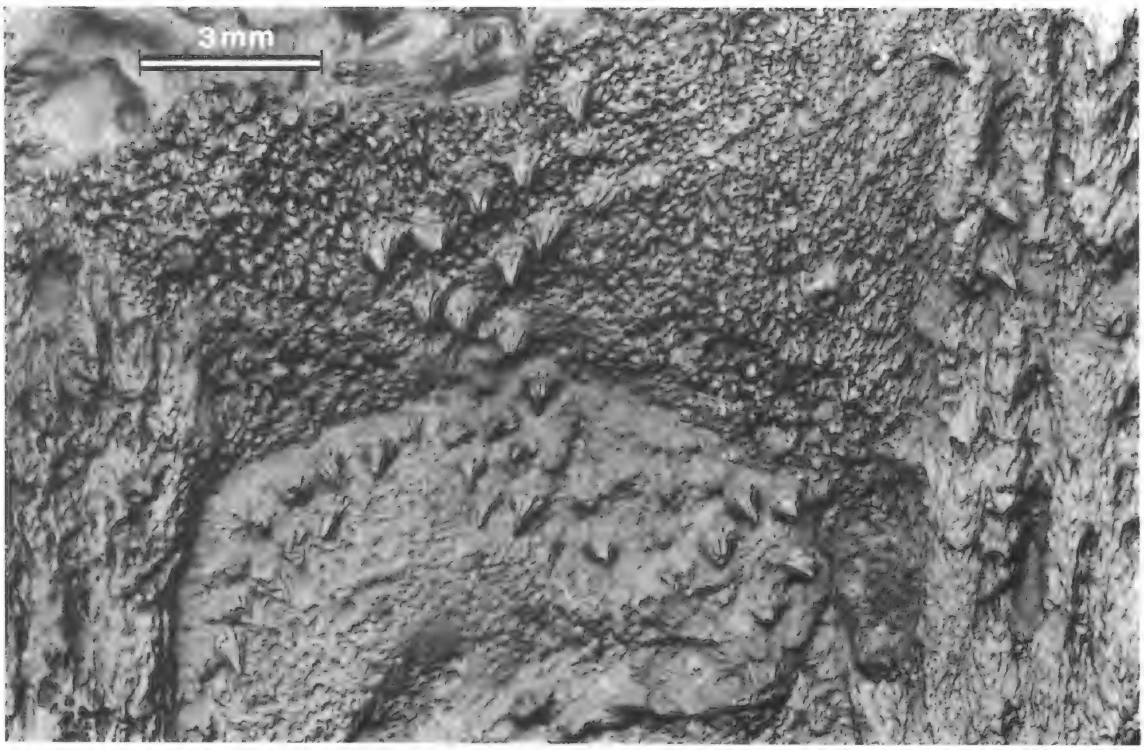


FIG. 22. *Hybodus basanus,* BM(NH) P6356, detail of endolymphatic fossa, scales, and muscle fibers. Anterior toward top of figure.

H. basanus in shape" (Patterson, 1966, p. 295).

Variation in the number of accessory cusps in teeth of AMNH 4692 is shown in figure 20. The dentition is separated into four components (upper, lower; left, right), and adjacent replacement series are numbered from front to back. Within each series teeth are numbered labio-lingually. For each tooth accessory cusps are counted both anterior and posterior to the principal cusp. A blank space indicates that the tooth is missing from the replacement series. Short dashes indicate that a tooth is present but the accessory cusps could not be counted.

The data show that accessory cusp number varies not only from one series to the next, but is sometimes extremely variable within a given series, e.g., upper right row 8; lower right rows 4, 8; lower left rows 4, 5. Moreover in AMNH 4692 the cusp number is asymmetrical, so some teeth in upper left rows 5 and 6 and lower left rows 1, 4, and 5 have up to four accessory cusps on either side of the principal cusp, whereas no teeth on the right side have this many accessory cusps. In upper left row 5 there may be up to four posterior accessory cusps. The number of accessory cusps often increases within a replacement series (e.g., lower left anterior accessories, row 1; posterior accessories, row 5; all accessories, row 4), but cusp numbers may also decrease (e.g., lower right anterior accessories, row 2). Comparable variation has not been reported in modern sharks, but it was found in some *Carcharias* jaws examined by the author.

The teeth in figure 18 are drawn to scale. Note that lower left and right anterior teeth are disparate in size, with much larger anteriors in the left ramus. Left and right teeth are of equivalent size only after row four. This curious abnormality has also been seen in BM(NH) P6356, which suggests that the size difference is genetically controlled and that many *H. basanus* specimens from Coo-

den may be from a single original interbreeding population.

The fourth series of upper left teeth in AMNH 4692 is interesting as the teeth are abnormally shaped. The outermost tooth is incomplete, but its cusps are twisted and gnarled, while its base is very poorly formed. The succeeding tooth in the series is also incomplete, but it had normal posterior accessory cusps. Lying between these two teeth, and extending between two teeth of the adjacent (preceding) series is an isolated, abnormal tooth. Its cusps are twisted, but not so badly as the first tooth of row four.

Teeth of the fifth lower left series are also malformed, but only the largest anterior accessory cusp is affected. The cusp is reflected outward (labially) in the first tooth. In the second and fourth tooth this cusp is only slightly out of line with the others, and in the third tooth it is normal. Variation of this kind within a replacement series has never been reported in modern sharks. In *Hybodus basanus* this variation suggests that "mistakes" sometimes occurred when tooth germs were being formed within the dental lamina, but that these "mistakes" could be "corrected" and could even recur. This contrasts with the fairly widespread tooth reversal phenomenon of some modern sharks, which is apparently irreversible (Gudger, 1937; Compagno, 1967; Reif, 1978a, 1980). Tooth reversal has not been found in *H. basanus.* Reif (1980) has suggested a mechanism for tooth reversal, in which a polarized tooth germ is split in such a way that the polarity of one part is reversed. There is some evidence from the alignment of teeth in the fourth upper left series of AMNH 4692 that a tooth germ was split, but there is no evidence for this in the fifth lower left series. Unless the tooth germ is irreversibly split, there seems to be a reasonable chance that localized disturbances in the dental lamina can be corrected, unless the cause of the disturbance is persistent (such as the way the teeth interlock) or is under genetic control.

Scales

The head of *Hybodus basanus* is covered by a shagreen of fine, pointed scales (figs. 21, 22). In addition, oropharyngeal denticles apparently lined much, if not all of the buccal cavity (fig. 7A). Morphologically there is little to distinguish them from body scales. In this respect, *H. basanus* differs from early hybodontids such as *H. delabechei* and *H. fraasi,* in which the squamation is differentiated into regions (Brown, 1900; Reif, personal commun.).

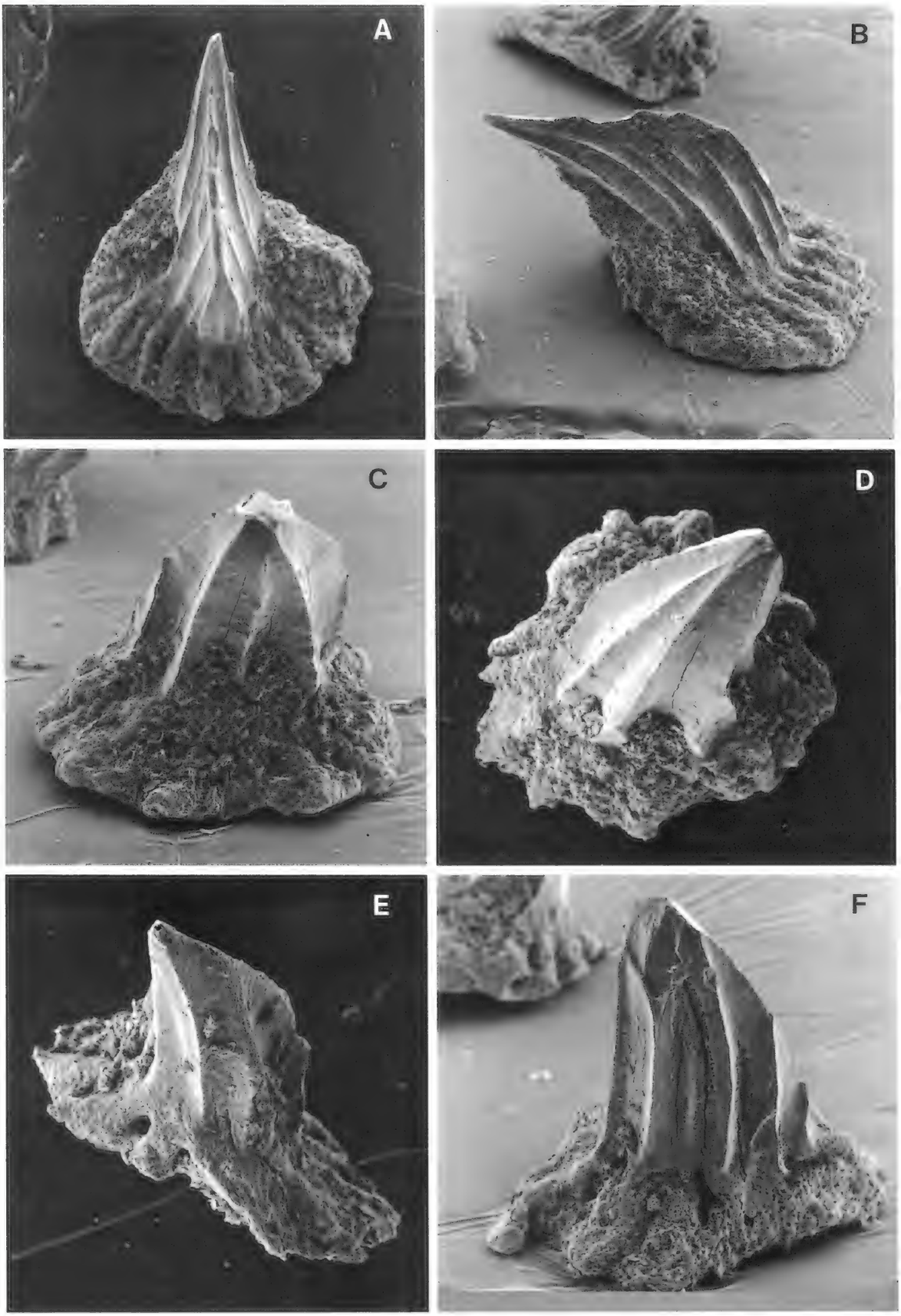
So far, only non-growing scales have been found in *H. basanus* (fig. 23). In this respect *H. basanus* resembles *H. fraasi* (Brown, 1900) but differs from earlier Jurassic hybodonts. Reif (1978b) found both growing and non-growing scales in *H. delabechei* and other species. The scale structure of *H. basanus* is otherwise typical of Mesozoic hybodontids. The cusp is ornamented by numerous longitudinal ridges. At the crown base are many neck canals, although a neck itself is not well developed (fig. 23E, F). The base is flat, slightly convex or concave, with several basal canals. It consists of a cellular bone but grades into osteodentine and ultimately into orthodentine in the crown.

The main variation of *Hybodus basanus* scales and oropharyngeal denticles is the acuity and curvature of their crowns. Oropharyngeal denticles from the front of the mouth are recurved posteriorly more than those nearer the jaw-joint, and have a slightly more attenuated crown.

Oropharyngeal denticles lining the roof of the buccal cavity are low-crowned, with a single strongly striated crown (fig. 23C, D). They are packed close together, only thinning out posterolaterally, where the skin was probably folded and loosely attached at the junction of the palatoquadrate and suborbital shelf. The dorsal surface of the "tongue" is also covered by dense scales, but these are slightly more acuminate. These scales lay not only over the hyoid arch, but extended back

→

FIG. 23. Scanning electron microscope photographs of *Hybodus basanus* scales (courtesy of W. E. Reif, Tübingen). Neck canals visible in (e) and (f). (a, b) body scale from corner of mouth, in (a) anterior and (b) right lateral view. (c–f) oropharyngeal scales; (c, d) scale in (c) posterior and (d) coronal view; (e, f) other scales in posterolateral views. Approximately ×75.


A
B
C
D
E
F

over the basibranchial region. In general appearance the oropharyngeal scales of *H. basanus* are reminiscent of Paleozoic "*Petrodus*" scales.

According to Nelson (1970), pharyngeal denticles are primitively distributed throughout the oropharyngeal region of gnathostomes, a condition which persists in a variety of neoselachians, e.g., *Notorhynchus maculatus, Ginglymostoma cirratum, Chlamydoselachus anguineum.* In some neoselachians, especially triakids and carcharhinids, denticles are absent from much of the dorsal region of the oropharynx, except on the "tongue" and overlying the branchial arches as pharyngeal pads. As far as the roof of the buccal cavity and region behind the hyoid are concerned, *H. basanus* conforms to Nelson's presumed primitive condition, although it has not been possible to determine denticle distribution farther back in the vicinity of the visceral arches.

Body scales from near the corner of the mouth are strongly recurved posteriorly, and have several axial ridges (fig. 23A, B). Scales from around the orbits and dorsal region are of two types. Some have a stout crown with a few prominent ridges, whereas others have a laterally compressed, bladelike crown with a semi-serrated crest and several moderate lateral ridges. The latter pattern resembles the growing scales of earlier hybodontids. It has not been possible to ascertain the precise arrangement of body scales in *H. basanus* except in the parietal region of BM(NH) P6356 (fig. 22) where they are spaced apart fairly evenly.

Finspines and Ceratotrichia

Displaced finspines are associated with some *Hybodus basanus* heads, e.g., inside the oropharyngeal region of BM(NH) P6356. The finspines are of typical hybodontid form (Maisey, 1975, 1978), with axial ribbing anteriorly and laterally, a double row of posterior hook-denticles, and a gently convex posterior spine wall which is open basally for about half the length of the spine. Finspines of BM(NH) P6357 (Woodward, 1891, pl. 1; 1916, fig. 5) closely resemble those associated with heads. It is, however, very difficult to establish conspecificity. Ceratotrichia are exposed in the dorsal fins of BM(NH) P6357, but are so poorly preserved as to have been overlooked by Woodward (1891, 1916).

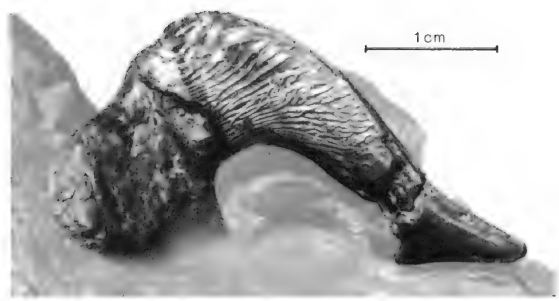


FIG. 24. *Hybodus basanus* cephalic spine, from BM(NH) P11817. British Museum (Nat. Hist.) photograph.

Cephalic Spines

In *Hybodus basanus* there is one cephalic spine on each side of the head, near the base of the postorbital process (fig. 24) and dorsal to the lateral otic process. These spines apparently occur only in males (Woodward, 1889b, 1916; Brown, 1900; Koken, 1907). Not all specimens are preserved well enough to determine whether they bore cephalic spines. The following specimens either had spines or a cartilaginous boss to support one: BM(NH) P11872, BM(NH) P6103, BM(NH) P11871 (figured by Woodward, 1916), BM(NH) P60110.

DISCUSSION

Relatively few fossil sharks are known well enough for their cranial anatomy to be compared with *Hybodus basanus.* Although detailed anatomical knowledge of modern sharks is now much improved over just a few years ago, information concerning the cranial morphology of fossil representatives of extant elasmobranch groups is virtually nonexistent. We know much more about the neurocranium of *Hybodus, Xenacanthus,* and *Tamiobatis* than about late Jurassic hexanchoids and heterodontids. When other Paleozoic sharks are considered along with *Xenacanthus* and *Tamiobatis* (e.g., "*Cladodus,*" *Cladoselache, Tristychius,* and *Cobelodus*), it becomes evident that available data are distributed through geological time rather like

sand in an hourglass, with *Hybodus basanus* representing virtually all the middle ground. Under these circumstances it is hardly surprising that *Hybodus* has historically been credited with some intermediate status between Paleozoic and modern sharks (e.g., Woodward, 1886a, 1886b; Zittel, 1911; Berg, 1955; Schaeffer, 1967). Unfortunately this situation remains essentially unchanged. The odds are fairly good that as the only Mesozoic shark known in detail, *Hybodus* is more closely allied to modern forms than the Paleozoic ones, and previous authors have mostly sought to confirm such a view.

Simply considering only those sharks whose cranial anatomy is known in some detail, Schaeffer (1981, fig. 26) produced a hypothesis of relationship in which *Xenacanthus, Tamiobatis, Ctenacanthus,* and "*Cladodus*" belong to a sister group of *Hybodus* and modern elasmobranchs. Schaeffer (*ibid.*) regarded two cranial characters as synapomorphies of *Hybodus* and modern elasmobranchs, namely the presence of an ectethmoid process (his character no. 6), and the position of the occipital arch "not projecting behind capsules and with most . . . occipitospinal nerves leaving braincase through vagus canal" (Schaeffer's character no. 19b).

Schaeffer (1981, p. 48) argues that the "ectethmoid process" of placoderms (e.g., Stensiö, 1963; Goujet, 1975; Young, 1980) actually correspond to the ethmoid articulation of *Xenacanthus* (and presumably of *Hybodus*). From Schaeffer's *Xenacanthus* material it is not possible to determine whether an orbitonasal canal (and, by implication, a *planum antorbitale* lateral to it; DeBeer, 1931) is present. In PU 22391, however, there is a canal which seems to correspond with the orbitonasal canal of *Hybodus* and modern sharks (fig. 13, fonv). Thus in *Xenacanthus* and *Hybodus* there appears to have been a cartilaginous *planum antorbitale* which could give rise to an ectethmoid process.

Comparison between the occipital regions of *Hybodus, Xenacanthus,* and modern sharks (e.g., fig. 15; for the purpose of this discussion, *Tamiobatis* and *Xenacanthus* are similar) suggests that their arrangements are fundamentally different (see earlier discussion). The occipital arch in modern elasmobranchs is almost completely flanked by the otic capsules. Spino-occipital nerves exit from the braincase mostly via the vagus canal (Schaeffer, 1981, p. 59). In *Xenacanthus, Tamiobatis,* and *Hybodus* only the anteriormost part of the occipital arch lies between the otic cap-

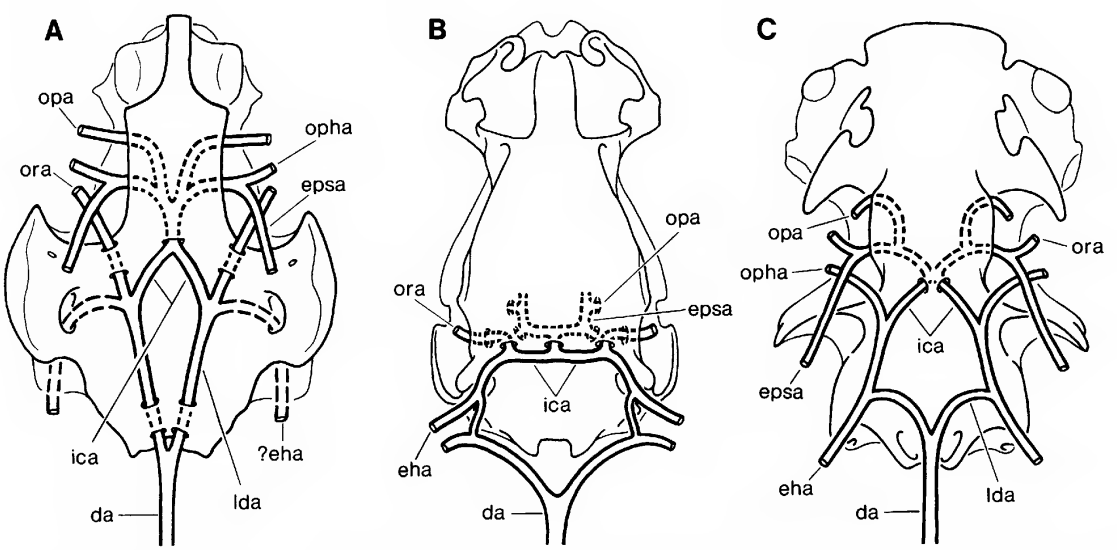


FIG. 25. Basicranial circulation in (a) *Hybodus basanus* (hypothetical); (b) *Heterodontus* (from dissections); and (c) *Chlamydoselachus* (after Allis, 1923).

sules. As Schaeffer (1981) noted, the extent to which the occipital segment is so situated is greater in *Xenacanthus* than in *Tamiobatis.* I do not find appreciable differences in the extent to which the occipital arch extends between the otic capsules in *Xenacanthus* and *Hybodus*; the main difference here is the retention of an open otico-occipital fissure by *Xenacanthus.* It was noted earlier that BM(NH) P50869, a lower Jurassic hybodont, has several spino-occipital nerves, and that *H. basanus* is similar. In BM(NH) P60110 (*H. basanus*) and also in BM(NH) P2203d (*H. reticulatus*), two or three ventral spino-occipital nerves emerge on the lateral surfaces of the occipital arch, essentially behind the vagus-glossopharyngeal fossa. It is concluded that the apomorphic features noted by Schaeffer (1981) in the occipital arch of modern elasmobranchs are not found in *Hybodus.*

Are there any cranial characters of *Hybodus* and modern elasmobranchs that can be recognized as synapomorphies of these forms? The inadequacy of the selachian fossil record makes it hard to determine whether any of the similarities between neurocrania of *Hybodus* and modern sharks can be regarded as synapomorphies. There is some evidence to suggest that a persistent adult otico-occipital fissure was more widespread than Schaeffer (1981) proposed. The condition of this character in *Cladoselache* (his outgroup to all other sharks) is unknown. It is possible that closure of the otico-occipital fissure in adult *Hybodus* and modern sharks is an apomorphic condition. *Hybodus* and modern sharks would be separated from *Xenacanthus* by formation of a discrete glossopharyngeal canal, which may (e.g., *Hybodus, Chlamydoselachus*) or may not be confluent with the vagus canal.

The present study of *H. basanus* does not contradict the majority of Schaeffer's (1981) general conclusions regarding chondrichthyans, but a few comments on some of his 20 cranial characters (listed below) are called for:

1. Prismatic calcification seems to be a chondrichthyan synapomorphy. Multiple layering of the prismatic tissue is much more widespread than was originally thought, however.

2. Presence of an open otico-occipital fissure is more widespread among Paleozoic sharks than previously thought.

4. The rostrum of modern sharks may not correspond to the "rostrum" of *Xenacanthus,* as suggested by Schaeffer (1981). The latter structure corresponds closely with the internasal keel of *Hybodus,* which is ventral to the rostral bar at the anterior margin of the precerebral fontanelle.

5. The posterior rim of the precerebral fontanelle is notched (probably for a pineal organ) in some well-preserved specimens of *Xenacanthus* (figs. 11, 14B). Paired foramina (interpreted as openings for the anterior cerebral veins) are situated in the fontanelle floor of *Hybodus* and *Xenacanthus,* suggesting that not all this region was originally extracranial.

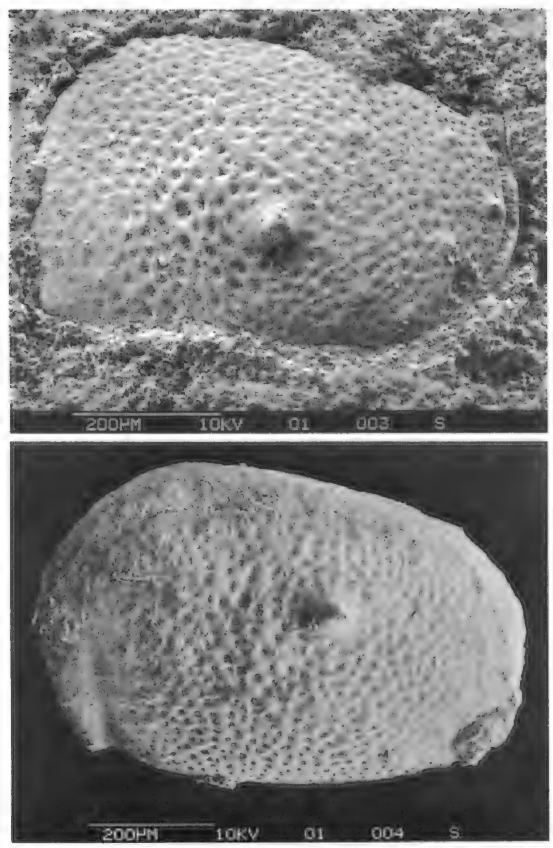


FIG. 26. Scanning electron microscope photographs of ostracods identified as *Cypridea wicheri torosa,* from a *Hybodus basanus* head, BM(NH) 40718.

6. An ectethmoid process as in modern sharks was probably present in *Xenacanthus, Hybodus,* and *Tristychius.*

12. Although Schaeffer (1981, p. 52) mentioned the presence of a distinct perilymphatic fenestra and endolymphatic foramen in *Hybodus,* these structures are not well defined and remain uncertain.

13. The morphology and occurrence of the hypotic lamina and glossopharyngeal canal has already been discussed; the latter is potentially useful as a synapomorphy of *Hybodus* and modern sharks, but requires further outgroup testing.

Since *Hybodus basanus* is at present the only Mesozoic shark in which the cranial anatomy is known in any detail, it is perhaps inevitable that this form will be subject to considerable scrutiny by those who wish to study elasmobranch phylogeny. It is hoped to continue the present study, in order to establish the extent to which *H. basanus* is representative of Mesozoic hybodont sharks. The recent discovery of hybodont-like sharks in Carboniferous rocks generates the possibility that *Hybodus* and its Mesozoic allies are only remotely related to modern elasmobranchs, and perhaps other Paleozoic sharks are more closely related to modern ones than is *Hybodus.*

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